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Pacific Island Flying Foxes: Proceedings of an International Conservation Conference

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Pacific Island Flying Foxes: Proceedings of an International Conservation Conference

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Contents

Part 4. Policies and Protection

Part 5. Education and the Future

Preface

These proceedings are a result of the Pacific Island Flying Fox Conference on 1–2 February 1990. The conference was hosted by Bat Conservation International, with funding from the Lubee Foundation, in Hawaii. This gathering was motivated by growing international concern about extinctions of and declines in flying fox populations throughout the Pacific. The principal problem has been the commercial hunting of bats throughout much of the Pacific and trade into Guam and the Mariana Islands, where bats are eaten as a delicacy.

This meeting was designed to help people from the islands secure a better future for bats and the ecosystems they inhabit. Participants were invited from around the world and included wildlife managers from the islands, conservationists, and scientists familiar with Pacific bats. Addresses of invited participants and contributors are provided to aid in communication about flying fox issues.

Part 1 provides background information for the subsequent sections. Part 2 discusses threats to island bat populations, while Part 3 provides status reports from selected islands. Part 4 furnishes information about local and international policies and regulations concerning flying foxes. Part 5 emphasizes the importance of education in the conservation of Pacific island flying foxes, and provides a general model for a public awareness campaign that can be modified to meet local island conservation, education, and cultural needs. Finally, there is a brief description of the Flying Fox Action Plan being prepared by the International Union for Conservation of Nature and Natural Resources.

For more information about flying foxes or bat conservation, please contact Bat Conservation International, P.O. Box 162603, Austin, Texas 78716.

Part 1.

Background Considerations

The Biology of Flying Foxes of the Genus *Pteropus:* A Review

by

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Introduction

With over 50 species, *Pteropus* is by far the largest genus among the flying foxes (Family Pteropodidae). For the species on which some recent information is available, a dismaying number are apparently undergoing population declines. At least three species have become extinct since the late 1800's; others are severely threatened. Most have limited island distributions, and are affected to varying degrees by direct exploitation, habitat alteration, and introduced predators. Yet these animals play an important, perhaps essential, role in forest ecosystems as pollinators and seed dispersers for many trees. Major reductions or extinction of flying fox populations would presage decreases in forest regeneration and diversity, and reduced productivity or decline of many plants economically important to man.

This conference was convened partly in response to the effect a luxury food market in Guam and the Commonwealth of the Northern Mariana Islands (CNMI) has had on Pacific island flying fox populations and to regulation of the trade under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). It also provides an opportunity to consider broader issues of flying fox conservation and management. This review attempts to summarize the biological data most relevant to the conservation of *Pteropus*, both the primary taxon in the commercial trade and the only flying fox on many of the smaller Pacific islands. The compilation also should provide easier access to the scattered literature on natural history.

Natural History

Reproduction

There is little variation in the reproductive pattern among the 23 species of *Pteropus* for which some information is now available. Adult females generally have only one young per year, with a gestation of 140–192 days (4.6–6.3 months). Although the young may begin to fly at 3 months, they usually are not weaned until they are 4–6 months old, and may remain dependent on their mothers for a year. Animals do not reach sexual maturity until they are 1.5–2.0 years old (Falanruw 1988).

This pattern is central to the problem of effectively conserving flying foxes—their maximum rate of population growth is low for a mammal of this size. Comparison with the common commensal rats (genus *Rattus*) makes this clear (Table 1).

Table 1. *Population parameters for the flying fox,* Pteropus, *and the rodent,* Rattus *(Nowak and Paradiso 1983; Falanruw 1988).*

Population parameters	*Pteropus*	*Rattus*
Gestation length (days)	140–192	21–30
Litter size	1	8
Interbirth interval (days)	180–360	28
Maximum number of litters per year	2	13
Age of sexual maturity (months)	18–24	3–5
Maximum life expectancy (years)	31	4

Rats reproduce at an age of 3–5 months and produce as many as eight young every 28 days (Nowak and Paradiso 1983). As a consequence, beginning with one pair of *Pteropus* and one pair of *Rattus* and assuming zero mortality, at the end of 1 year there would be 3 (maximally 4) bats, and about 4,000 rats.

In analyzing timing of reproduction in pteropodids, Baker and Baker (1936) noted a strong seasonality for births, with young born about March–April north from latitude 4° N and about September south from latitude 3° N. Incorporating subsequent information from additional species, it is possible to see this pattern does not hold completely (Table 2). Births do seem to be highly synchronized and seasonal for most species, with births generally occurring during the first half of the year at north latitudes, and during the second half of the year at south latitudes. There is also an indication that the birth peak shifts with latitude in some of the more widely distributed species (e.g., *P. giganteus* in India; Tidemann 1985). Some striking exceptions to this overall pattern (e.g., *P. melanotus natalis* and *P. scapulatus*) are also evident.

A few species (e.g., *P. mariannus yapensis* in Yap, possibly *P. molossinus* in Pohnpei, and *P. tonganus* in Samoa) may have more than one birth peak per year. Only one species, *P. mariannus mariannus* in Guam, seems to be truly aseasonal, with young found in the population every month of the year (Wiles 1987a). Falanruw (1988) observed postpartum estrus in *P. m. yapensis*, and suggested that this species may have two young per year. *Pteropus rodricensis* seems to have only one young per year in the wild, but in captivity is capable of producing one young every 9 months (West 1986).

Aseasonality or multiple birth peaks do not necessarily mean that an individual female produces more than one young per year. With an average pregnancy of 4–6 months and a rearing interval of 4–6 months, it is likely that for most species, each female has only one young per year. Even a postpartum estrus is not unequivocal evidence for multiple annual births, since a number of bat species, including some pteropodids, display various delay mechanisms during pregnancy (e.g., *Eidolon helvum* [Mutere 1967] and *Haplonycteris fischeri* [Heideman 1988]). Additionally, West (1986) noted that in the captive colony of *P. rodricensis*, individual females tend to give birth every alternate birth cycle.

Longevity and Survivorship

Survival rates of *Pteropus* in the wild are unknown, but the maximum life span for a captive animal is greater than 31 years (Nowak and Paradiso 1983). Heideman and Heaney (1989) studied three species of small pteropodids in the Philippines. They found that *H. fischeri*, the species which was reproductively mature at the greatest age (12 months) and had the fewest young per year (one), lived the longest, possibly reaching 13 years. Since no *Pteropus* species is known to be sexually mature before 18 months, their expected survivorship would likely be considerably longer.

Bat mortality rates are generally highest for juveniles (Tuttle and Stevenson 1982), but no data are available for *Pteropus*. Data for *H. fischeri* suggest a minimum juvenile mortality rate of 10–30% during the first two-thirds of lactation (Heideman and Heaney 1989). Much higher mortality rates are reported for juvenile Microchiroptera (Tuttle and Stevenson 1982). Average estimated subadult–adult survivorship for three species of small pteropodids varied from 60 to 80% (Heideman and Heaney 1989).

Roosting Ecology

Habitat Requirements

There are often marked differences, both geographically and ecologically, between roosting and feeding habitats for *Pteropus*, although on small islands such distinctions are more limited. Also, the habitat chosen for roosting varies considerably among *Pteropus* species. Some seem restricted altitudinally. *Pteropus livingstonei* in the Comoro Islands (Cheke and Dahl 1981) and *P. leucopterus* of the Philippines (Heaney et al. 1987) are found only in native montane forest, whereas *P. rufus* in Madagascar (Anderson 1912) and *P. griseus griseus* on Timor (Goodwin 1979) occur primarily in coastal forests. *Pteropus phaeocephalus* from the Mortlock Islands in Chuuk and *P. howensis* from Ontong Java (Sanborn and Nicholson 1950) live on barely emergent coral atolls.

Species also show a range of tolerance for human habitat alteration. Many species roost mainly in primary forest, such as *P. niger* on Mauritius (Cheke and Dahl 1981), *P. ornatus* in New Caledonia (Sanborn and Nicholson 1950), *P. pumilus* in the Philippines (Heaney et al. 1987), *P. samoensis* in Samoa (Cox 1983), and *P. tonganus* on Niue (Wodzicki and Felten 1975). Others, such as the Philippine *P. vampyrus* (Heideman and Heaney

Table 2. *Seasonal pattern of births for species and subspecies of* Pteropus *by latitude.*

Latitude	Taxon	Months with births reported												References
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
20° N	*giganteus giganteus*	*	*	*										Moghe 1951; Neuweiler 1969; Roberts 1977
13° N	*vampyrus lanensis*				#	#								Heideman and Heaney 1992
13° N	*hypomelanus cagayanus*				#	#								Heideman and Heaney 1992
13° N	*mariannus mariannus*	*	*	*	*	*	*	*	*	*	*	*	*	Wiles 1987a
9° N	*mariannus yapensis*		#	#	#		#		#	#	#			Falanruw 1988
8° N	*melanotus melanotus*			*										Andersen 1912
7° N	*molossinus*		*						#	#		#		Jackson 1962
5° N	*giganteus ariel*				*	*								Andersen 1912; Dolbeer et al. 1988
5° S	*howensis*									*	*			Sanborn and Nicholson 1950
6° S	*neohibernicus*						#	#	#					Smith and Hood 1981
9° S	*seychellensis aldabrensis*											*	*	Cheke and Dahl 1981
10° S	*melanotus natalis*	*	*	*										Tidemann 1985
10° S	*rayneri cognatus*											#		T. Flannery, personal communication
12° S	*livingstonei*								*	*	*			Cheke and Dahl 1981
12° S	*seychellensis comorensis*									*	*	*		Cheke and Dahl 1981
14° S	*tonganus tonganus* (Samoa)	#							#		#			Personal observation
14° S	*samoensis samoensis*						#	#	#					Personal observation
16° S	*tonganus geddei* (Vanuatu)								*	*				Baker and Baker 1936
16° S	*anetianus*								*	*				Baker and Baker 1936; Sanborn and Nicholson 1950
16° S	*voeltzkowi*						#							Kingdon 1974
17° S	*conspicillatus conspicillatus*										*	*	*	McGuckin and Blackshaw 1985; Martin et al. 1987
19° S	*tonganus tonganus* (Niue)						#	#			#			Wodzicki and Felten 1975
19° S	*rodricensis*									*	*	*	*	Carroll 1981; Cheke and Dahl 1981
20° S	*tonganus tonganus* (Cook Islands)							*	*					Wodzicki and Felten 1980
20° S	*alecto gouldi*			#										McGuckin and Blackshaw 1985; Martin et al. 1987
21° S	*ornatus ornatus*										#			Sanborn and Nicholson 1950
21° S	*subniger*										*			Moutou 1982
21° S	*niger*										*			Moutou 1982
25° S	*scapulatus*			*	*									McGuckin and Blackshaw 1985; Martin et al. 1987
28° S	*poliocephalus*									*	*			Martin et al. 1987

[a] * = seasonal limits known.
[b] # = seasonal limits undefined.

1992) and the four Australian species (*alecto, conspicillatus, poliocephalus,* and *scapulatus*), can be found in a variety of anthropogenic habitats, but rely heavily on native forest for either roosts or food (Nelson 1965b; McWilliam 1985–86; Heideman and Heaney 1992). *Pteropus hypomelanus* in the Philippines is most common in disturbed, agricultural plots (Heideman and Heaney 1992). A few species, when protected, roost in trees or forest remnants in populated areas, such as *P. tonganus* at the Kolovai Sanctuary in Tonga, *P. poliocephalus* at Ku-ring-gai in the suburbs of Sydney, Australia (Anonymous 1987), and *P. giganteus* in certain towns and villages in southern India (Marimuthu 1988).

Roost Sites

Pteropus is distinguished among the Megachiroptera by its tendency to form large aggregations on exposed tree branches. Marshall (1983) reviewed flying fox roosting habits, and found that of the 42 genera, only 4 roost in this fashion. Seven form colonies in caves or rock shelters, and the remaining 16 for which information is available roost singly or in small scattered groups in trees.

Most *Pteropus* species roost in emergent trees, which rise above the forest canopy. A large fig tree, the banyan (*Ficus prolixa*) and the she-oak, *Casuarina* spp., are frequently cited as roost trees: for example, *P. mariannus* on Guam (Wiles 1987a), *P. giganteus* in India (Marimuthu 1988), *P. melanotus natalis* on Christmas Island (Tidemann 1985), *P. ornatus* in New Caledonia (Sanborn and Nicholson 1950), and *P. tonganus* in Samoa and Vanuatu (Chambers and Esrom 1988, personal observation). However, many other canopy and sub-canopy trees are used, including *Guettarda speciosa, Mammea odorata, Cananga odorata, Cerbera manghas, Homalium acuminatum, Pisonia* sp., and *Aleurites moluccana* (Sanborn and Nicholson 1950; Wodzicki and Felten 1980; Tidemann 1985; Wiles 1987a).

Mangrove swamps are also important roosting habitat, at least on a seasonal basis, for a number of species: for example, *P. molossinus* on Pohnpei (Coultas 1931), *P. mariannus yapensis* on Yap (Falanruw 1988), *P. melanotus melanotus* in the Nicobar Islands (Anderson 1912), *P. vampyrus edulis* in Timor (Goodwin 1979), *P. lylei* in Thailand (Lekagul and McNeely 1977), and all four Australian species (Ratcliffe 1931, 1932; Nelson 1965b).

Two exceptions to the canopy roosting behavior have been reported. *Pteropus alecto* from Australia, although usually a tree-dwelling species, has been found in a natural limestone tower in Queensland (Stager and Hall 1983), and *P. subniger*, now extinct, from Mauritius and Reunion, lived in colonies of up to 400 in large tree hollows (Cheke and Dahl 1981).

Common to many roosts are topographic features that provide protection from strong winds and give animals easy access to updrafts for flight (Cheke and Dahl 1981; Nicoll and Racey 1981). Kingdon (1974) speculated that the preference of *Pteropus* for bare, upper branches of very tall trees might be influenced by the animal's large size, and the need for a "free-fall take off." Roosts are also often found near ridgetops. For example, all known roost sites for *P. m. mariannus* are within 100 m of the 80–180-m-high cliff line on northern Guam (Wiles 1987a).

Thermal characteristics may also be important. Advani (1982) argued that the thick foliage of preferred roost trees for *P. giganteus* in India protects the bats from the heat of the sun. Likewise, Ratcliffe (1932) and Sanborn and Nicholson (1950) concluded that shade was important to Australian and New Caledonian species. More commonly, however, roosts are located on relatively bare branches, in almost full sunlight.

Pteropus species show considerable fidelity to traditional roost sites. If unmolested, colonies, like the one protected by the royal family on Tonga, can be found at the same site year after year. Wiles (1982) noted that the site used by *P. m. mariannus* on Guam in 1982 had been used off and on by the colony for a number of years, and that all roost sites used by the animals in fiscal year 1981 were previously used (Wiles 1981). Certain camps in India (McCann 1934) and Australia (Tidemann 1985) have been used for at least 60 years.

Human disturbance, however, particularly hunting, may cause colonies to move. Falanruw (1988) reported that *P. m. yapensis* displayed increased roosting in mangroves with increased hunting pressure. Colonies of *P. tonganus* on Tutuila, American Samoa, move roost sites frequently, but often relocate within the same general area or move to another traditional site (Pierson and Rainey, personal observation).

Colony Size

The relationship between colony size, and temporal and spatial patterns of food availability is not well understood. Although the genus *Pteropus* is thought of as colonial, not all species exhibit the same degree of coloniality. Many roost in very

small groups or alone (Table 3). For some species, roosting patterns seem consistent over time, but for others, currently observed patterns, particularly small maximum colony size, may reflect some combination of ongoing disturbance by hunting and population reduction. Assessments of coloniality based on one or a few seasonally clustered observations may not be reliable, for reasons given in the subsequent sections.

A few species, such as *P. lylei* (Lekagul and McNeely 1977), *P. scapulatus*, and *P. vampyrus*, historically have formed exceedingly large aggre-

Table 3. *Roosting habits of* Pteropus *species.*

Species	Locality	Reference
Strongly Colonial		
P. ornatus	New Caledonia	Sanborn and Nicholson 1950
P. subniger	Mauritius	Cheke and Dahl 1981
P. mariannus yapensis	Yap	Falanruw 1988
P. m. ualanus	Kosrae	Personal observation
P. m. mariannus	Guam/CNMI	Wiles 1987a
P. m. paganensis	CNMI	Wiles et al. 1989
P. tonganus geddei	Vanuatu	Baker and Baker 1936
P. t. tonganus	Tonga, Samoa	Personal observation
P. rufus rufus	Madagascar	Andersen 1912
P. seychellensis seychellensis	Seychelle Island	Racey 1979
P. s. comorensis	Comoro Island	Cheke and Dahl 1981
P. voeltzkowi	Pemba Island	Seehausen 1991
P. melanotus melanotus	Nicobar Island	Andersen 1912
P. m. natalis	Christmas Island	Tidemann 1985
P. rodricensis	Rodrigues Island	Pook 1977
P. molossinus	Pohnpei	Jackson 1962
P. lylei	Thailand	Lekagul and McNeely 1977
P. giganteus ariel	Maldives	Andersen 1912
P. g. giganteus	India	Andersen 1912; Moghe 1951
P. vampyrus lanensis	Philippines	Heideman and Heaney, 1992
P. v. edulis	Timor	Goodwin 1979
P. alecto gouldi	Australia	Nelson 1965b
P. conspicillatus conspicillatus	Australia	Ratcliffe 1932
P. neohibernicus neohibernicus	Papua New Guinea	McKean 1972
P. poliocephalus	Australia	Nelson 1965a, 1965b
P. scapulatus	Australia	Nelson 1965a, 1965b
Moderately Colonial		
P. hypomelanus cagayanus	Philippines	Heideman and Heaney, 1992
P. mariannus pelewensis	Palau	Perez 1968
P. m. ulthiensis	Ulithi Atoll	Wiles et al. 1991
P. tonganus tonganus	Niue	Wodzicki and Felten 1975
P. niger	Mascarenes	Cheke and Dahl 1981
P. anetianus	Vanuatu	Chambers and Esrom 1988
P. insularis	Chuuk	Personal observation
Solitary or Small Groups		
P. giganteus ariel	Maldives	Phillips 1958, 1959
P. pumilus	Philippines	Heideman and Heaney, 1992
P. griseus griseus	Timor	Goodwin 1979
P. livingstonei	Comoro Islands	Cheke and Dahl 1981
P. rayneri grandis	Bougainville	McKean 1972
P. samoensis nawaiensis	Fiji	G. Graham, personal communication
P. s. samoensis	Samoa	Cox 1983
P. temmincki capistratus	Bismarck Archipelago	T. Flannery, personal communication

gations. Ratcliffe (1932) reported a colony of *P. scapulatus* in Queensland, Australia, in the 1930's that probably numbered in the millions. Reports from the same era in the Philippines document a mixed colony of *P. vampyrus* and *Acerodon jubatus* of about 150,000 (Taylor 1934). Now, the maximum colony size for *P. scapulatus* is around 100,000 (Richards 1983), and for *P. vampyrus* in the Philippines around 500–1,000 (Heideman and Heaney 1992).

A number of other species also seem to be strongly colonial, but form much smaller aggregations, with colony size rarely exceeding a few thousand, and more typically being a few hundred: for example, *P. giganteus giganteus* in India and Pakistan (Neuweiler 1969; Roberts 1977), *P. m. mariannus* on Guam (Wiles 1987a), *P. melanotus natalis* on Christmas Island (Tidemann 1985), *P. rodricensis* on Rodrigues Island (Pook 1977), *P. s. seychellensis* in the Seychelles (Racey 1979), and *P. t. tonganus* in Samoa (Pierson and Rainey, personal observation).

Research has traditionally focused on colonial species, whose high visibility provides relatively favorable study conditions. A few more poorly known species have been identified as either solitary or forming predominantly very small groups (Table 3). Phillips (1958, 1959) described *P. giganteus ariel*, which is colonial elsewhere, as "always solitary in Addu Atoll." Goodwin (1979) stated that no camps have been reported for *P. griseus griseus* on Timor, and that "solitary individuals were found hanging well-hidden beneath the leaves of species of *Corypha* and *Borassus* in coastal palm forests." McKean (1972) reported that *P. rayneri grandis* was found roosting, usually singly, in tall trees in secondary forest on Bougainville. *Pteropus temmincki capistratus* of the Bismarck Archipelago is either solitary or roosts in male–female pairs (T. Flannery, personal communication). Heideman and Heaney (1992) presumed that *P. pumilus* in the Philippines roosts singly or in small, inconspicuous groups. It was caught with some regularity in mist nets in primary and secondary forest, but the only individual observed roosting was in a canopy tree fern (*Cyathea*). *Pteropus samoensis samoensis* in Samoa roosts singly, in pairs, or in small groups (Cox 1983), but is most often found in pairs.

No information is available on almost three quarters of all *Pteropus* species. While it is possible to confuse rarity with noncoloniality, it seems likely that some of the species known from only a very few specimens may, if they still exist, be noncolonial. Likely candidates are *P. gilliardi*, known from a single specimen collected in montane forest on New Britain in the Bismarck Archipelago in 1958 (Van Deusen 1969); *P. leucopterus*, known from very few specimens collected on forested ridgetops on a few islands in the Philippines (Heideman and Heaney 1992); and *P. tokudae*, last seen in 1968, now presumed extinct on Guam (Wiles 1987a), but considered very rare by local people many years ago.

A few species seem to be only moderately colonial. *Pteropus insularis* from Chuuk form small colonies (up to 100) at traditional locations, but individual animals are also found scattered throughout the forest (Bruner and Pratt 1979; personal observation). A recent survey by Wiles et al. (1991) on Ulithi suggested a similar situation for *P. mariannus ulthiensis*. Similarly, for *P. niger* on Mauritius, in 1978, there were a few colonies of several hundred, but most bats seemed to be spread through the forested areas in small groups of between 1 and 15 (Cheke and Dahl 1981). On Palau in 1967, all the *P. mariannus pelewensis* seen were either roosting or flying alone, or less commonly were in groups of two to four (Perez 1968). *Pteropus anetianus* roosts in small, quiet groups (Chambers and Esrom 1988). *Pteropus hypomelanus cagayanus* in the Philippines is found roosting in tall trees or coconut palms in groups of a few to several hundred (Heideman and Heaney 1992).

As noted earlier, human disturbance may have altered roosting patterns for some populations. On Niue, for example, *P. t. tonganus*, which is strongly colonial elsewhere in its range (e.g., *P. t. geddiei* on Vanuatu and New Caledonia, or *P. t. tonganus* on Samoa and Tonga), roosts singly, in pairs, and rarely in larger groups of up to 100. The population has been significantly reduced by deforestation and overhunting (Wodzicki and Felten 1975). Similarly for the same subspecies on Mangaia in the Cook Islands, the current maximum observed colony size is fewer than 20 individuals (D. W. Steadman, personal communication).

Seasonal Changes in Roost Composition

At least five species show rather dramatic seasonal changes in roost composition. *Pteropus t. geddiei* in Vanuatu (Baker and Baker 1936) forms large mixed-sex colonies near the shore from September to January. Females leave the camps in February, when they become pregnant, and are difficult to find until June, when they form single-sex inland camps to give birth to their young. The

males continue in the coastal camps from January to June, but from June to September seem to be dispersed and are difficult to find. Likewise for *P. melanotus natalis* on Christmas Island, females live in the deeper part of the forest when pregnant, and 9 out of 10 animals captured near the coast at this time are males (Tidemann 1985).

In Australia, colony size for three species, *P. poliocephalus*, *P. alecto*, and *P. scapulatus*, seems correlated with food abundance (Nelson 1965b), with animals forming camps at times of peak flowering, and dispersing when food is scarce. *Pteropus poliocephalus* forms both summer (September–January) and winter (April–September) camps at different localities, with the summer camps being much larger. Although Nelson (1965b) found *P. scapulatus* to form exceedingly large aggregations from November to February, with dispersal into smaller groups the rest of the year, a more recent study (McWilliam 1985–86) documented the persistence of large colonies into May in New South Wales. Maximum colony size for *P. alecto* occurs in the summer months of November–December.

Social Structure of Roosts

The limited available data suggest a considerable range of social systems among *Pteropus* species. (Although there is no evidence of this for flying foxes, it should be remembered that social systems, too, may change with population density and food availability). Harem formation may be fairly common among colonial species and has been documented for *P. seychellensis comorensis* (Cheke and Dahl 1981), *P. rodricensis* (Carroll and Mace 1988), and *P. m. mariannus* (Wiles 1987a). Wiles (1987a) reported that in the only remaining colony of *P. m. mariannus* on Guam, about 80% of the animals roost in harems throughout the year, with harem groups consisting of a single dominant male and 2–15 females. While males retain exclusive breeding rights to a particular group of females and defend their harem against intruding bachelor males, the females do not show loyalty to the males, and the number of females within the group may vary from day to day. Most of the bachelor males roost in a large group, associated with the main colony.

Although Neuweiler (1969), in a study of *P. giganteus* in India, did not specify harem formation, he observed a vertical rank order for males within a colony, with the more dominant males defending positions near the top of the tree. During the mating season, the young males roost in a separate tree, and the females gather together in the upper branches with the dominant males.

Preliminary data indicated that *P. s. samoensis* form pair bonds (Cox 1983; personal observation). Although the duration and exclusivity of these associations is not known, roosts typically consist of an adult male, an adult female, and one young.

The most comprehensive study of *Pteropus* behavior was conducted by Nelson (1965a), primarily on *P. poliocephalus*. This species forms summer camps from September to April or June. Summer camps contain both sexes, are where young are born and raised, and are where mate selection takes place and conception occurs. Winter camps, which are occupied from April or June to September, are sexually segregated and contain mostly immature animals.

When summer camps first form the sexes tend to be segregated, pregnant females associating with each other until they give birth to a single young sometime between late September and late October. The females devote the months of October–December primarily to caring for the young. During December and January, mate selection takes place, with males establishing territories and becoming more aggressive toward other males during February. During March and April, there are four different social groupings within the camp: **family groups**, which consist of a monogamously paired male and female, plus the female's offspring from the previous breeding season; **adult groups**, which differ from family groups in that the males may be either monogamous or polygamous, and there are no juveniles present; **guard groups**, comprised of animals that act as sentinels for the camp and roost around its periphery; and **juvenile packs**, consisting of mostly young, nonreproductive males, and a few adults. Conception occurs in late March, and shortly thereafter the two sexes segregate, and the camps begin to disperse.

Mother–Young Interactions

Newborn *Pteropus* are sparsely haired and dependent on their mothers to maintain their body temperature (Bartholomew et al. 1964). They cling to mother's abdomen and are carried for several weeks (Nelson 1965a; Neuweiler 1969; Roberts 1977), using special hook-like growths on the inside curve of the claw (Nelson 1965a) and probably the hook-like milk teeth to hold on to the mother's fur. For *P. poliocephalus*, the young can-

not fly until they are 3 months old, but at about 3 weeks of age, they are left behind when their mothers go out to feed (Nelson 1965a). Infant mortality is probably highest at this point because the young are more vulnerable to predation (Wiles 1987a) and are susceptible to falling below the canopy, where the females are reluctant to retrieve them (Nelson 1965a). Although the young may be weaned at 4–6 months, they will often remain associated with their mothers for at least 1 year.

There is some evidence that during the weaning period, the mothers feed the young mouth to mouth. This has been observed in captive *P. rodricensis* (Pook 1977) and captive *P. m. mariannus* (J. S. Villagomez, personal communication).

Feeding Ecology

Bat–Plant Interactions

Bats are pollinators and seed dispersers for many plants throughout the tropics (Fleming and Heithaus 1981; Marshall 1983; Cox et al. 1992; Wiles and Fujita 1992). Only one group of Megachiroptera, the Macroglossinae, seems to be strictly nectarivorous; the other groups are more catholic in their diet. All species of *Pteropus* studied feed both on nectar and fruit of a wide variety of plants. Several species have also been observed consuming leaves.

Presumably during long evolutionary association, certain plants seem to have adapted morphologically to facilitate and, in some cases, require pollination or seed dispersal by bats. "Bat flowers" typically open and produce nectar only at night. They tend to be white and strongly scented, are often pendulous or brush shaped, and are located away from the foliage, easily accessible to aerial visitors. "Bat fruits" are drab and usually have a strong, distinctive odor that is distasteful to man. They are generally large, with a large seed, are also located away from the foliage, and remain attached to the tree after maturity (Marshall 1983).

Despite this apparent evolutionary pattern, many plants that fit these models are exploited by other animals, while many plants used by bats do not fit (Stashko and Dinerstein 1988). For example, the silk cotton tree, *Ceiba pentandra*, morphologically a perfect bat plant, is pollinated by one flying fox species, *P. tonganus*, in Samoa, but attracts a whole host of pollinators in continental areas (Elmqvist et al. 1992). The figs (*Ficus* spp.), some of which do not fit the bat plant model particularly well, are a major food resource for numerous bird and mammal species, including bats.

Bats can be dispersal agents in two ways. For large-seeded fruits, the bats may carry the fruit some distance from the parent tree, where the fleshy parts are consumed and the seed discarded. Bats are capable of carrying considerable weight in flight, and on many oceanic islands they may be the only vertebrates capable of carrying very large-seeded fruits. For small-seeded fruits, seed-containing fragments or the entire fruit may be ingested and the seeds dispersed in orally ejected pellets of fiber and other bulky fruit components or in feces. Studies with both New and Old World fruit bats have shown enhancement of germinability for seeds that have passed through the digestive tract (Fleming and Heithaus 1981; Utzurrum and Heideman 1988).

Feeding Behavior

Information on feeding behavior is available for about half the species of *Pteropus*. These 27 species exploit flowers, fruits or leaves of plants from 50 plant families and 92 genera (Ratcliffe 1932; McKean 1972; Roberts 1977; Goodwin 1979; Dobat and Peikert-Holle 1985; Marshall 1985; Tidemann 1985; McWilliam 1985–86; Flannery 1990; Wiles and Fujita 1992). Data on the diets of *P. mariannus* on Guam and Yap; *P. melanotus natalis* on Christmas Island; *P. tonganus* in the Cooks, Niue, and Samoa; and *P. samoensis* in Samoa; and the four Australian species (Ratcliffe 1931, 1932; Wodzicki and Felten 1975, 1980; Tidemann 1985; McWilliam 1985–86; Wiles 1987a; Falanruw 1988; Richards 1990; Cox et al. 1992) are substantial, but a thorough investigation of the feeding ecology of any one species remains to be done.

Although the *Pteropus* species that have been studied feed on a wide variety of fruits and flowers, individual species, through a preference for certain foods on a seasonal basis, are likely to be "sequential specialists" (Marshall 1983): for example, *P. tonganus* on *Ceiba* (Wodzicki and Felten 1980; Elmqvist et al. 1992), *P. melanotus natalis* on *Muntingia* (Tidemann 1987), and *P. samoensis* on *Freycinetia reineckei* (Cox 1984a). Particularly in island settings with low floral diversity, certain plant species, which provide reliable maintenance resources during seasons of low food availability (Terborgh 1986), may be essential to the survival of the flying foxes and other frugivores. One concern regarding large-scale alteration of a single

habitat type, such as the clearing of lowland forest, is the potential loss of such critical plant species.

Most *Pteropus* are primarily nocturnal, and most plants relying on bats for pollination are night flowering. Nevertheless, in the relatively predator-free environment of oceanic islands, some species have become partially or entirely diurnal: for example, *P. melanotus natalis* (Tidemann 1987), *P. niger* (Andersen 1912), *P. molossinus* (Jackson 1962, personal observation), *P. insularis* (personal observation), *P. seychellensis* (Andersen 1912), *P. seychellensis comorensis* (Cheke and Dahl 1981), *P. hypomelanus maris* (Phillips 1958), and *P. samoensis samoensis* (Cox 1983).

Many *Pteropus* species tend to feed on conspicuous, clumped, and locally abundant resources (Marshall 1983), and will often form noisy feeding groups, with intense displays of competition. Data are insufficient to evaluate the relation between coloniality and aggregated foraging behavior, but some colonial species are known to forage in groups (e.g., *P. tonganus* on Samoa [personal observation] and the Australian species [Ratcliffe 1932]), whereas the more solitary species are often observed feeding alone. Group foraging is most evident for plentiful food resources. For example, in Samoa, a large *Ficus* tree with abundant fruit or a *Ceiba* in full flower will attract numerous *P. tonganus* in a single night, whereas a flowering coconut tree (*Cocos nucifera*) is visited by the occasional individual.

Foraging areas are almost always separated from roosting areas. On large land masses, animals may travel 40–60 km (Roberts 1977; Marshall 1983) to reach a feeding area. Colonies roosting on off-shore islands often travel a number of miles across water to mainland foraging sites (Allen 1940). On isolated, oceanic islands, animals tend to feed more locally; nevertheless, there may be significant distance and elevational difference between roosting and feeding habitats.

Causes of Mortality

Though information on age structure and estimates of age-specific mortality rates for *Pteropus* are lacking, the long life span and low reproductive rate clearly indicate animals with an evolutionary history involving low levels of natural mortality. In this section we review two sources of natural mortality, predation and typhoons, and how human activity has altered their effect; the limited but striking evidence for mass mortalities from epidemic disease; and the more direct effect by man through hunting and habitat alteration. Hunting and habitat alteration usually occur simultaneously and only occasionally can their relative contributions to population declines be teased apart.

Predation

Large bats, particularly on islands, have relatively few predators other than man. Within the range of *Pteropus*, the only significant predators identified are raptors and snakes (Gilette and Kimbrough 1970). On the more isolated oceanic islands, such as Samoa, Tonga, and the Federated States of Micronesia, there are no known predators.

The best data on bird predation comes from Fiji, where flying fox remains were found in 56% of pellets taken from peregrine falcon (*Falco peregrinus*) eyries in rainforest habitat (White et al. 1988). In Australia, wedge-tailed eagles (*Aquila audax*) and white-breasted sea eagles (*Haliaeetus leucogaster*) have been observed attempting to catch flying foxes, and will elicit an alarm cry from the bats (Nelson 1965a). The bat hawk, *Machaerhamphus alcinus*, although it occurs within the range of *Pteropus*, is generally reported preying on smaller microchiropterans (Francis 1985).

Snakes are potential predators for many species of *Pteropus*, but are not known to have a significant effect on any population, except that of *P. m. mariannus* on Guam. There, the brown tree snake, *Boiga irregularis*, accidentally introduced after World War II, has caused the decline or extinction of several endemic birds (Savidge 1987), and is likely responsible for the lack of recruitment in the remaining *P. m. mariannus* colony. Wiles (1987b) noted that in 1982, 46.6% of all young counted were judged to be large-sized, but in 1984–86, after the snake had moved into the area, no bats of this size class were observed. He suggested that the snake preys on young *Pteropus* which have become too large to be carried by their mothers, when they are left in the roosts alone at night. Given the damage done to the vertebrate fauna of Guam by *B. irregularis*, its abundance on the island, and the importance of Guam as a regional military and commercial shipping hub, its introduction and establishment on other islands is a significant threat. Other less well-studied, related snakes pose similar risks (Greene 1989).

In Australia, both pythons (*Morelia* spp.) and larger monitor lizards (*Varanus* spp.) are known to

feed on flying foxes (Nelson 1965a). Arboreal monitor lizards were widely introduced on Micronesia and are established, but not abundant. Their effect on co-occurring *Pteropus* is not known.

Typhoons

Severe tropical storms are a recurring phenomenon throughout much of the range of *Pteropus*, and periodically affect particularly island faunas in both the Pacific and Indian Ocean regions (Robertson 1992). The risk of severe population reductions or extinction is increased on islands that have already experienced extensive deforestation and population reduction (Wiles 1987b). For example, *P. rodricensis* on Rodrigues Island is confined to a single colony in one small patch of remnant forest. In 1979, Typhoon Celine II decreased the number of animals from 151 to 70 (Carroll 1984). There are reports of storm mortalities or population reductions following typhoons for *P. niger* on Mauritius (Cheke and Dahl 1981), *P. samoensis* and *P. tonganus* on Samoa (Daschbach 1990), and *P. m. mariannus* on Guam (Wiles 1987a).

Evidence from the Marianas (P. Glass, personal communication), Samoa (Daschbach 1990; B. Landin, personal communication), and Vanuatu (Chambers and Esrom 1988) suggested, however, that a major cause of storm-related mortality for flying foxes is intensified post-storm hunting. Defoliation reduces concealment of roosting animals, so that they are more readily detected and killed by persons actively hunting them. Storm damage also decreases food resources, so flying foxes forage more diurnally and are less cautious in entering plantations and villages—areas they would typically enter after dark. This greatly increases the probability that they will be noticed and killed opportunistically.

Following an intense typhoon in February 1990, domestic animals (dogs, cats, and pigs) were reported to kill large numbers of *P. tonganus* in Samoa (Lundgren, personal communication). The bats were foraging for fruit on the ground or in fallen trees in the villages, generally at night. Being unable to take flight from the ground, they were extremely vulnerable to predation. Since cats and pigs also forage extensively in the forest, the mortality was probably greater than that directly observed.

Epidemics

Few data are available on diseases in flying foxes. The problems most commonly noted for zoo animals are nonlethal cold-like symptoms (Carpenter 1986). There are, however, scattered reports of severe epidemics decimating wild populations, and more have emerged in response to inquiries. The first comes from the Whitney Expeditions in the early 1930's. During a 2-month survey of Kosrae in the Caroline Islands, a research team located only four flying foxes (*P. mariannus ualanus*), and learned from residents that the animals had all died in a recent epidemic associated with an outbreak of measles in the human population (Coultas 1931). Degener (1949) described a similar epidemic depleting *P. tonganus* populations near Savu Savu in Fiji sometime before 1949. Flannery (1989) reported two recent epidemics, one in 1985 affecting *P. neohibernicus hilli* on Manus, Admiralty Islands, and the other, *P. rayneri grandis* in Bougainville and Buka, Solomon Islands, in 1987. It is noteworthy that the other species on Manus, *P. admiralitatum*, was unaffected, as were populations of *P. neohibernicus* on nearby islands. Flannery (personal communication) also found evidence of another epidemic on Choiseul, Solomon Islands. The cause of these epidemics is unknown, but the high fatality rate suggested to Flannery that the responsible agent may have been introduced by domestic animals or humans.

Overhunting

Flying foxes have long been a dietary component for some Pacific island cultures. Historically, when the animals were taken by traditional means (e.g., sticks, stones, or hooked vines), hunting did not seem to threaten the survival of populations (Cox 1983; Chambers and Esrom 1988). This perception is partly corroborated by the archaeological record, which shows numerous extinctions or local extirpations of land and sea birds associated with early human settlement, but, currently, only Tonga has a record of flying fox extinctions (Steadman 1989 and personal communication). Now, increasingly extensive hunting with firearms, and generally rising human densities have paralleled marked population declines of *P. m. mariannus* on Guam and the CNMI (Wiles 1987b; Wiles et al. 1989; Lemke 1992a, 1992b), *P. voeltzkowi* on Pemba Island (Seehausen 1991), *P. seychellensis* from the Seychelles (Racey 1979), *P. t. tonganus* on Niue (Wodzicki and Felten 1975), and several spe-

cies in the Philippines (Heaney and Heideman 1987). Overhunting is thought to have been the primary cause of extinction for *P. subniger* on Mauritius more than 100 years ago (Moutou 1982), and for at least three other pteropodid species in recent years (*P. tokudae* on Guam [Wiles 1987b], *Aproteles bulmerae* in PNG [Flannery 1989], and *Dobsonia chapmani* in the Philippines [Heaney and Heideman 1987]).

To further avoid such losses, the effect of hunting for local consumption deserves periodic monitoring, even in areas where no crisis is evident. Although no trends in bat populations were reported, a survey of residents in Vanuatu revealed that 85% of the respondents regarded flying foxes as an important food item (Chambers and Esrom 1988). Flying foxes also occasionally appear in the Port Vila market and are served at local tourist hotels. There is reason for concern in Samoa, where bats are commonly eaten, particularly in the less westernized sections of Western Samoa. There local chiefs report that accessible bat populations began to decline with the introduction of firearms. Cultural recognition of the ecological importance of flying foxes provides a vehicle, however, for instituting village controls on excessive take, as has been done now in two areas of Savai'i, Western Samoa (Cox and Elmqvist 1991).

From the perspective of a flying fox population, there may be little to differentiate hunting for consumption from killing for pest control. The extent to which flying foxes are viewed as pests varies with the crops grown, cultural preferences for extent of tree ripening, stringency of cosmetic standards for cash crops, and closeness of the human population to fully exploiting the tree crop resource. A recent symposium in Australia includes several papers on flying fox cash crop depredation and control measures, emphasizing non-destructive methods (Fleming and Robinson 1987; Hall and Richards 1987; Loebel and Sanewski 1987; Tidemann and Nelson 1987).

On islands where habitat alteration has progressed to the point that bats and humans feed on a largely overlapping set of plants and increasing human demand exceeds available crop production, extinction through depredation control becomes a prospect. Dolbeer et al. (1988) described efforts to control perceived damage to coconuts by *P. giganteus ariel*, a local endemic, in the atolls of Republic of the Maldives. In demonstration efforts, they killed an estimated 55–79% of the bats on three islands, leaving 16–67 bats in those populations. These population sizes and plans for expanding depredation control leave long-term survival of the flying foxes in doubt. Similar resource conflicts may exist on densely populated atolls in the eastern Solomon Islands (W. King, personal communication). Particularly given possible offsetting, but rarely recognized, ecologic and economic benefits of flying foxes (Cox et al. 1992; Wiles and Fujita 1992), it is important that the damage attributed to them be carefully assessed before systematic lethal control programs are undertaken.

Commercial trade

In recent years, a significant threat to flying fox populations in several areas of the Pacific has been commercial exploitation for a luxury food market in Guam and the Commonwealth of the Northern Marianas (CNMI; Wiles and Payne 1986; Brautigam 1988; Wiles 1992). As early as the late 1960's, following the depletion of its own flying fox resources, Guam began importing bats from a number of islands in the Pacific. Since 1975, Guam has recorded imports of as many as 29,554 in 1 year, and a total of 220,308 flying foxes (Brautigam and Elmqvist 1990; Wiles 1992). This trade had a significant effect on flying fox populations in Samoa in the early 1980's (Cox 1984b), and in the Federated States of Micronesia, particularly Chuuk and Pohnpei, in the late 1980's (Rainey 1990). The effects of the trade on Palau, which has been the largest and most consistent supplier, are unknown.

Although available information suggests Guam and the CNMI provide the only currently significant international market for flying foxes, limited trade does occur elsewhere in the Pacific. For example, Vanuatu exported 365 *P. tonganus* to Noumea, New Caledonia in 1989 and early 1990 (E. Bani, personal communication). Also, flying foxes are sold quite widely in local markets in Malaysia and Indonesia, where individual vendors report selling 2,000–9,000 flying foxes per year, and claim colonies are getting more difficult to find (Fujita 1988).

Deforestation

Loss of native forest poses a significant threat to flying fox populations on many Pacific and Indian Ocean islands by destroying food resources and roosting habitat. This may come about incrementally through small-scale agricultural conversion or rapidly in large blocks (e.g., export timber sales or extensive cash crop plantings, sometimes associated with international aid programs). The resulting habitat varies in its residual value to

flying foxes. Mixed agroforest and coconut monocultures are used, the former preferentially by some species; pastures and some tree monocultures (e.g., conifers) offer nothing. Forest clearing is often accompanied by road construction, which provides easier access to remaining roosting and foraging areas for hunters (Falanruw 1988).

The deleterious effects of forest clearing are documented for *P. rodricensis* in the Mascarenes (Cheke and Dahl 1981; Carroll 1984), *P. voeltzkowi* on Pemba Island (Seehausen 1991), *P. livingstonei* in the Comoros (Cheke and Dahl 1981), and *P. tonganus* on Niue (Wodzicki and Felten 1975), the Cooks (Wodzicki and Felten 1980), Samoa (Cox 1983, 1984b), and probably the Solomons (Flannery 1989). On Rodrigues Island, for example, bats are found in one of only two significant areas of remaining forest. Of 35 endemic plant species originally found on the island, only 17 remain (Carroll 1984). Forest clearing has eliminated stands of tamarind, the pods of which are a favored food item for the bats (Cheke and Dahl 1981). *Pteropus livingstonei* on the Comoros is confined to forested, mountain areas of Anjouan Island, where two-thirds of the forest was lost between 1968 and 1974 (Cheke and Dahl 1981). The extinction of *Dobsonia chapmani* noted above, and declines in other species, such as *P. vampyrus*, are attributable in part to the loss of forest in the Philippines, where, for example, primary forest cover on the island of Negros has been reduced from 60% to 6% (Heaney and Heideman 1987).

Dramatic declines in Australian flying fox populations in the past 50 years are likely more attributable to extensive forest clearing than to shooting, even though the latter has been energetically pursued. Remaining populations experience periodic severe food stress (through failure of normal flowering in native forest or loss of nectar through rain) that drives them to attempt to feed on virtually nonnutritive, unripe commercial fruit (Ratcliffe 1931; Nelson 1965b; Fleming and Robinson 1987; Tidemann and Nelson 1987). As forest reduction and fragmentation continues these events will recur or increase in frequency.

Population Dynamics

Unfortunately, the few *Pteropus* species and subspecies for which we have population estimates are those on the brink of extinction. The difficult task of counting relatively small animals in a rainforest is easier if most of the forest is cleared and there are few animals, preferably in one place (e.g., the situation for *P. rodricensis*). To maintain densities of flying foxes adequate to carry out their (as yet poorly delineated) ecological role as seed dispersers and pollinators and to maintain them as a resource in countries where they are consumed as food, it would be desirable to monitor population levels in a way that allows recognition of declines well before the situation is so extreme. For most species, available data regarding population trends are anecdotal. These anecdotes should not be discounted, particularly when they come from long-term observers, such as local hunters. Developing quantitative methods for monitoring flying fox populations is impeded by the lack of essential natural history information. Perceptions (or measures) of abundance can be influenced by seasonal (and multiannual) variations in movement patterns and the degree of population aggregation. Efforts to evaluate seasonal variation in abundance indices for pteropodids are to be welcomed (Craig and Syron 1992).

In several island groups flying fox populations declined when hunted for the market in Guam (Cox 1983; Wiles and Payne 1986; Falanruw 1988) and began to recover in Yap (but not in parts of the CNMI) after hunting for export was prohibited (Falanruw 1988). A complementary approach to predicting the effect of exploitation is to develop numerical population models using estimates of critical population parameters (birth rate, mortality rates, etc.). These models can be based on such flying fox data as are available, and harvest estimates. We include three examples as a demonstration, starting with what would happen to *P. insularis* populations in Chuuk with continuing heavy commercial harvest. Figure 1 uses a 1986 population estimate (Engbring, in correspondence) of 5,628 and projects the population trend, if the 1989 level of 2,507 exported to Guam (Brautigam and Elmqvist 1990) were maintained over several years. The simple deterministic computer model (Ferson et al. 1989) assumes an 80% survivorship for all age classes. This includes two young per female per year, sexual maturity at age 2, equal numbers of males and females, and begins with a stable age distribution. Though these parameters are generally optimistic (e.g., as noted earlier most *Pteropus* have one young per year rather than two), the model population was extinct in 4 years.

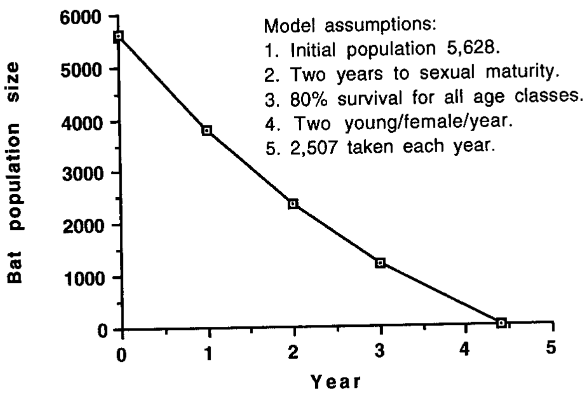

Fig. 1. Simulated population size trend for *P. insularis* in Chuuk, based on 1989 commercial export records (Brautigam and Elmqvist 1990; Wiles, in correspondence), and a 1986 population estimate (Engbring, in correspondence).

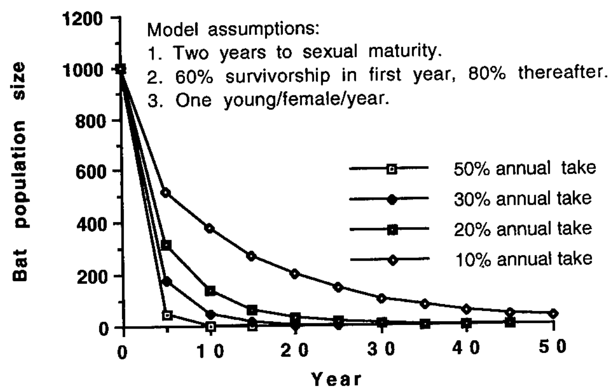

Fig. 2. Size trends for simulated *Pteropus* populations of 1,000 animals, with 10%, 20%, 30%, and 50% taken each year.

Using slightly more realistic assumptions (as before, except one young per year, 60% survivorship in the first year and 80% thereafter), Fig. 2 shows the effect of different levels of exploitation on an initial population of 1,000 flying foxes. Removing 50% of the population each year leads to extinction in 12 years. At 10%, 29 animals remain after 50 years. With the same assumptions, Fig. 3 shows the trends for populations of 10,000, 5,000, and 1,000 flying foxes with 20% killed per year. After 50 years, the population that began at 5,000 contains 1 animal and the population that began at 10,000 contains 2. There are obvious inadequacies in these models, but they serve to illustrate that flying fox populations will likely decline under relatively low rates of exploitation and will recover

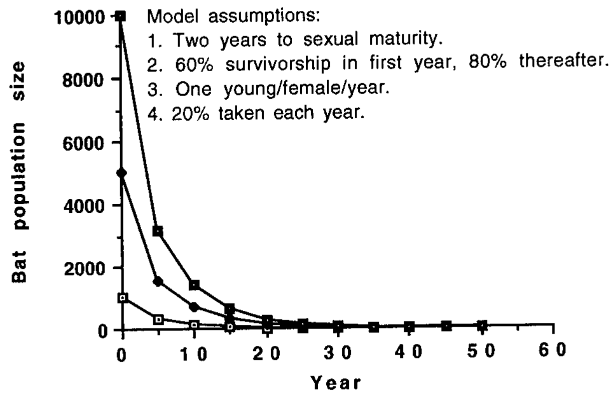

Fig. 3. Size trends for simulated *Pteropus* populations of 1,000, 5,000, and 10,000 animals, with 20% of the population taken each year.

slowly from natural or human-induced population reductions.

Conclusions

Low maximum reproductive rate is the primary feature of *Pteropus* that puts its species at risk as exploited in a world with increasingly efficient hunting technologies. The archaeological record, oral tradition, observations of living hunters, and some population data make it clear that for many Pacific flying fox species, the transition from viable to seriously declining populations is quite recent. The examples of decline and extinction provide an early warning to other countries that monitoring of populations and management intervention will likely be necessary to maintain flying fox populations.

The second critical feature of *Pteropus* biology is dependence of most species on tracts of native forest for roosting and feeding. The relationship is reciprocal in that flying foxes also help to maintain the forest. Given the seasonally irregular, geographically patchy patterns of fruiting and flowering in tropical forests, the foraging range of a *Pteropus* population is likely to be large. On the basis of other benefits (watershed protection and production of traditional resources, including food, medicinals, and building materials) the careful management of substantial areas of native forest is an important resource planning goal. Although much work remains in assessing habitat requirements, preserving forest will help conserve flying foxes.

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Flying Foxes as Pollinators and Seed Dispersers in Pacific Island Ecosystems

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Abstract. The role of pollinators and seed dispersers in oceanic islands is poorly understood, but recent botanical investigations have emphasized the importance of flying foxes in island ecosystems. Given the problems of highly endemic floras on oceanic islands, significant reproductive isolation of island plant populations, and extremely depauperate pollinator faunas, the conservation of flying foxes on islands becomes crucially important to the plant communities.

Autu. (This is a Samoan translation of the above abstract.) Ua le'i manino lelei le faia o manu 'ese'ese ma la'au i motu o le Pacifika, ae peta'i ua matua'i taua tele le tulaga o pe'a. E tele lava ituaiga 'ese'ese o la'au e mana'omia asiasiga o pe'a i fuala'au e fa'atupu ai fua ma la'au fou. O lona uiga la, ua matua taua tele lava le fa'asaoina o pe'a i motu o le Pasifika.

One of the first observations of flying fox pollination in the South Pacific occurred during the visit of the *S.S. Challenger* (one of the first sailing expeditions to the South Pacific) to the island of Tongatapu, Tonga, in the 19th century. The naturalist of the expedition, Moseley (1879), reported seeing flying foxes visit the bright red flowers of coastal trees. For several reasons it is significant that this, the second documented observation of bat pollination in the world (De la Nux previously mentioned pteropodid visits in a private letter), occurred in the South Pacific. Initially, reports by early explorers throughout the South Pacific indicate that there were high densities of flying foxes in the forests of Polynesia before European contact. In some cases the densities were so high that the distinctive

musky smell of flying foxes permeated the indigenous forests (Peale 1848). Secondly, the close ecological relations between flying foxes and the island floras, long known to the natives of the South Pacific, was clearly surprising to Europeans accustomed to temperate regions lacking phytophilic bats (Nicoll 1909).

Despite the unusual associations between bats and plants in the South Pacific, the possibility of plant dependence on flying foxes was ignored by zoologists, but attracted the attention of early botanists working in the palaeotropics, including Burck (1892), Porsch (1915, 1923), Cammerloher (1923, 1928), and, later, van der Pijl (1956), and Degener (unpublished field notes). Despite clear and convincing evidence of flying fox pollination of a number of plants, their work was largely ignored by the scientific community. For European workers accustomed to wind and insect pollination of temperate plants, the latter often involving intricate, tightly coevolved mechanisms, it was difficult to conceive of organisms the size of flying foxes regularly transporting pollen from flower to flower. The thought of bats, viewed with horror and suspicion by most European peoples, performing any useful role in nature was also inimical to the European consciousness. This cultural bias, coupled with the relative remoteness of the South Pacific islands and the lack of night-vision technologies, resulted in an unawareness of the importance of flying fox pollination and seed dispersal in the islands.

This lack of knowledge about the importance of flying foxes to plants was not shared, however, by the indigenous peoples of the South Pacific. The cultures and religions of these people were based on living in close harmony with the earth, and the role of flying foxes in the ecosystem was understood and appreciated (Sinavaiana and Enright 1992).

In this paper, we explore the question "What will happen to the Pacific forests if the flying foxes go extinct?" The importance of frugivores and vertebrate pollinators in structuring ecosystems is far greater in the South Pacific islands than elsewhere. Throughout western Polynesia, Micronesia, and Melanesia, megachiropteran bats of the genus *Pteropus* play important roles as pollinators and seed dispersers (Pierson and Rainey 1992; Wiles and Fujita 1992). A recent review indicates species of *Pteropus* to visit flowers of at least 26 different species and eat the fruits of at least 64 different species (Marshall 1985). Over 31 genera in 14 different angiosperm families are known to be pollinated by Megachiroptera (Marshall 1985). But the role of flying fox pollination and seed dispersal in Pacific island ecosystems must be considered in light of the unique characteristics of Pacific island floras.

Endemism and Vulnerability of Island Floras

Plant populations on remote oceanic islands are reproductively isolated from source floras, and from each other. This geographic isolation has significant consequences:

1. The various modes of long-distance dispersal favor specific types of plant breeding system, particularly inbreeding (Baker 1955, 1959, 1967; Stebbins 1957; Baker and Cox 1984; Cox 1991). Plants with obligate outcrossing systems such as gametophytic self-incompatibility (Anderson and Stebbins 1984) or dioecism (Bawa 1982; Baker and Cox 1984; Cox 1985) are less likely to establish breeding populations after long-distance dispersal, resulting in a sampling bias towards inbreeders or apomictic taxa in immigration events. However, outcrossing mechanisms in these populations may evolve later (Carr et al. 1986).
2. Low numbers of immigrants, infrequent immigration events, and small population sizes favor genetic drift and divergence from source populations.

These factors have undoubtedly played a role in the mosaic of high levels of endemism throughout oceanic floras. For the Pacific island archipelagos, typically 30–50% of the plants occur nowhere else. Their vulnerability to extinction resulting from extremely limited geographic ranges is exacerbated by dependence on a limited suite of pollinators and seed dispersers (Cox et al. 1991). For example, Cox (1983a) showed that *Freycinetia arborea*, a Hawaiian rainforest liana, depended for pollination on native honeycreepers that are now extinct. The plant itself was saved from extinction by an introduced bird, *Zosterops japonica*, which became the sole pollinator.

Flying Foxes as Pollinators and Seed Dispersers in Island Ecosystems

The importance of flying foxes as pollinators and seed dispersers in island ecosystems is illustrated by our ongoing studies in Samoa where

about 30% of the rainforest canopy trees rely, at least partially, on flying foxes for pollination or seed dispersal. Even though Samoa has only two flying fox species, *Pteropus samoensis* and *P. tonganus*, which are in many respects ecologically distinct, both feed on a wide range of flowers and fruits. We found *P. samoensis* to feed on the fruits of *Cupaniopsis samoensis* (Sapindaceae), *Ficus graeffii* (Moraceae), *Dysoxylum maota* (Meliaceae), *Planchonella* sp., *Fagraea beretiana*, and *Collospermum samoense* (Liliaceae; Cox 1983b, 1984); and the flowers of *Freycinetia reineckei*, *Canaga odorata*, and *Barringtonia asiatica*. In various islands of the South Pacific, *Pteropus tonganus* has been noted to feed on the flowers of *Ceiba pentandra* (Bombacaceae), *Cocos nucifera* (Palmae), and *Syzygium malaccense* and the fruits of *Syzygium jambos* (Myrtaceae), *Artocarpus altilis* (Moraceae), *Carica papaya* (Caricaceae), *Mangifera indica* (Anacardiaceae), *Musa paradisiaca* (Musaceae), *Artocarpus heterophylla* (Moraceae), *Inocarpus fagifer* (Leguminosae), *Syzygium malaccense, S. clusifolium, S. cuminii, S. richii, S. inophylloides* (Myrtaceae), *Psidium guajava* (Myrtaceae), *Ficus prolixa* (Moraceae), *Fagraea beretiana* (Loganiaceae), *Cerbera manghas* (Apocynaceae), *Persea americana* (Lauraceae), *Terminalia catappa* (Combretaceae), *Pandanus tectorius* (Pandanaceae), *Pometia pinnata* (Sapindaceae), *Ochrosia oppositifolia* (Apocynaceae), *Diospyros samoensis* (Ebenaceae), *Planchonella torricellensis* (Sapotaceae), and *Citrus sinensis* (Rutaceae; Sykes 1970; Wodzicki and Felten 1975, 1980; Cox 1983b).

While the pollination biology of most Samoan rainforest trees has not been investigated in detail, in a model study of the kapok tree, *Ceiba pentandra*, the flowers were visited predominantly by *P. tonganus* (Elmqvist et al. 1992). In continental areas, *C. pentandra* is visited by a diverse array of vertebrates and invertebrates (van der Pijl 1935; Baker and Harris 1959; Carvalho 1960; Janson et al. 1981).

Data on the phenology of the Samoan rain forest, and the complex role flying foxes play in this ecosystem, are scanty. The emerging picture, however, indicates that they have an extremely important role in maintaining forest diversity. Evidence for this was gathered by observing frugivore visitations to rainforest trees and by measuring bat-generated seed rain along transects in the forest. *Pteropus* species have a characteristic dentition that allows us to distinguish *Pteropus*-dispersed fruits from fruits dispersed by birds or introduced mammals (e.g., rats and pigs). Bat-generated seed rain densities away from roosts are as high as 36 fruits per square meter.

Extreme spatial and temporal variability are generally found in both the species composition of the seed rain and in densities. During the dry season (June to September) in 1988, the highest density of fruiting trees in western Savai'i (Fig. 1) was found on lowland hills (old volcano cones, 150–350 m above sea level, eight transects on four different hills sampled), whereas low densities were found in both the lowland rain forest (<150 m, eight transects) and in the highlands (>600 m, four transects). As lowland hills are scarce in the landscape, this suggests that during this season, the flying foxes may have to fly long distances (5–10 km or more) between patches of fruiting trees. Trees in the lowland forests began fruiting later (September–December), and this phenological asynchrony between habitats may provide the highly mobile flying foxes with a steady food resource.

The proportion of fruits in the seed rain samples that were dispersed by flying foxes in July 1988 varied between 0 and 100%, being particularly high for *Syzygium inophylloides*, *Planchonella torricellensis*, and *Inocarpus fagifer* (Fig. 2). The proportion was 80–100% in the lowland forest, where few trees were fruiting at that time. Some of these fruits were presumably trans-

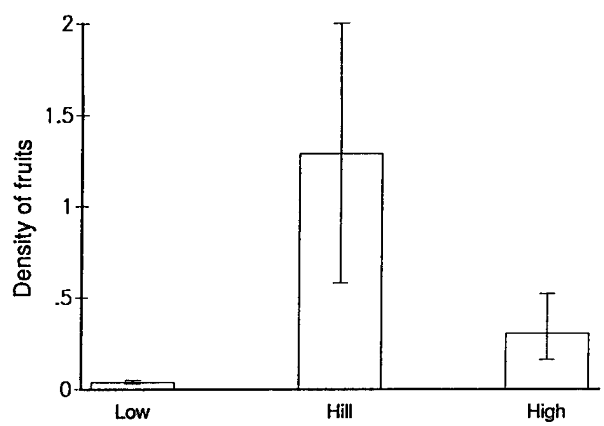

Fig. 1. The density per square meter of fleshy fruits found on the forest floor in three different habitats, lowland forest (<150 m above sea level), lowland hills (150–300 m) and highland forest (>600 m) on Savai'i, Western Samoa. Data from randomly distributed transects (100 m × 1 m) in July 1988. N = 8, 8, and 4, respectively. Mean and S.E. given.

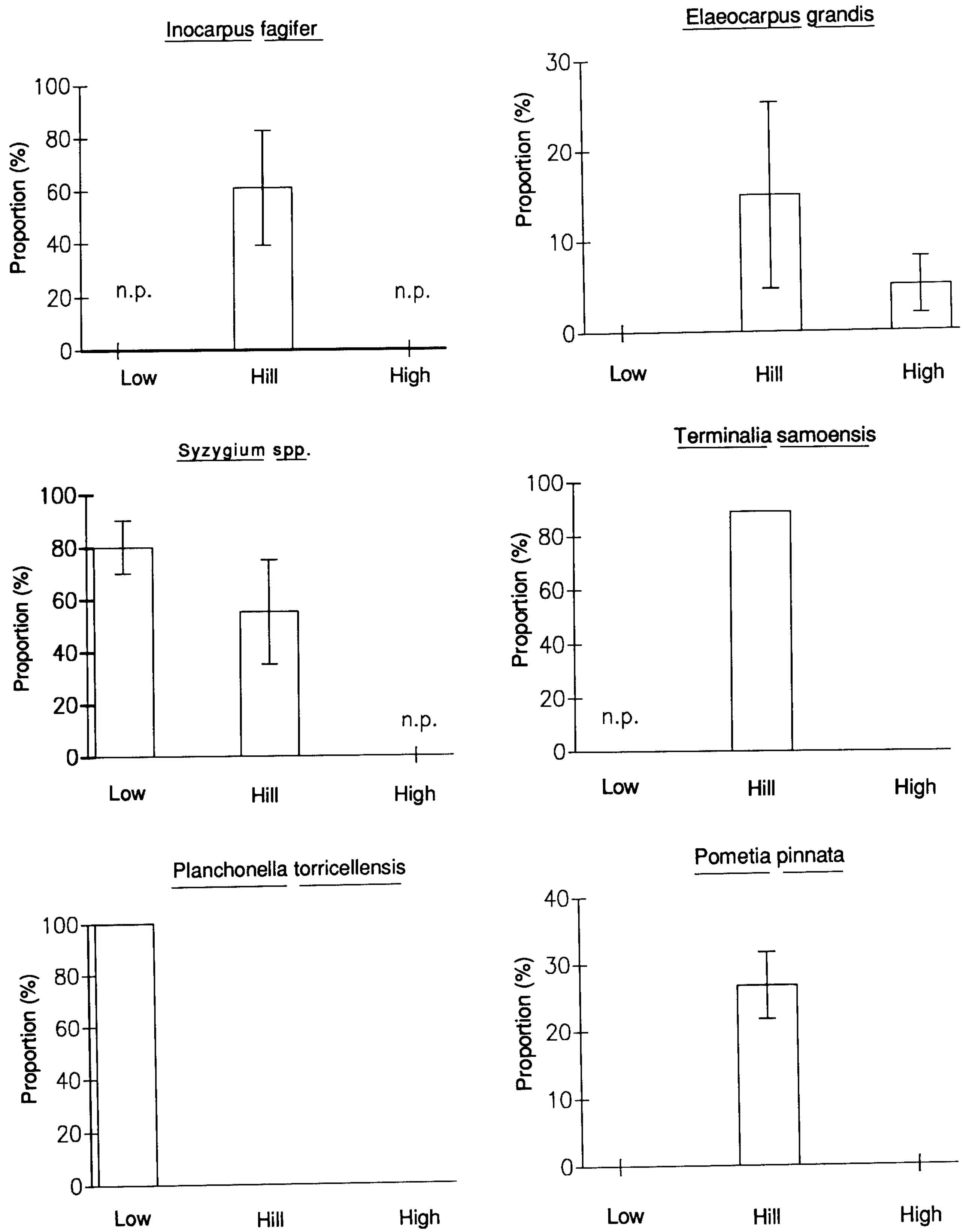

Fig. 2. The proportion of fleshy fruits from different rain forest tree species dispersed by flying foxes (as judged by teeth and punchmarks), found on the forest floor in lowland forest, lowland hills, and highland forest in July 1988. Data from transects (100 m × 1 m), N = 8, 8, and 4. Mean and S.E. given; n.p. = not present.

ported considerable distances from their mother trees on lowland hills (1–3 km). These data emphasize the importance of flying fox dispersal for gene flow patterns and long-distance dispersal. In general, seed dispersal by bats results in a more homogeneous seed rain than dispersal by birds (Fleming 1988). Bats contribute up to 95% of the seeds deposited in cleared open areas (Thomas et al. 1988), whereas birds deposit seeds in areas where they have perches (i.e., around fruiting trees and in mature forest undergrowth).

Conclusions

Many continental tropical areas often show very specialized, tightly linked plant–pollinator and plant–seed disperser relationships that enhance extinction risks for both participants. Our studies suggest that although such tight relations are not typical on oceanic islands, these systems are still highly vulnerable to extinction events because of the low diversity of pollinators and seed dispersers. In Samoa, the extinction of flying foxes would likely result in the gradual loss of a significant fraction of the rain forest canopy trees. This change in habitat structure and resource availability would inevitably have consequences for other members of the rainforest community (Myers 1986), including humans.

Recognition of the importance of flying foxes in the maintenance of viable rainforest communities underlines the need for both local and international monitoring and management of their populations. The 1989 decision by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to monitor and limit international trade in flying foxes (Bräutigam and Elmqvist 1990) is an important step, but for most species the persistence of ecologically significant populations will also require local protection and management.

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Food Plants and Economic Importance of Flying Foxes on Pacific Islands

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Abstract. We reviewed the zoological and botanical literature to document the food plants of flying foxes (Chiroptera: Pteropodidae) on Pacific islands. Our list of known bat foods contains 84 species of plants from 41 families, with species from the Myrtaceae, Moraceae, Anacardiaceae, Leguminosae, and Pandanaceae most common. A similar review of the products obtained from these plants was also conducted to determine the economic effect of bat-plant interactions in the region. The three largest categories of products derived from bat-visited plants are timber and other items made from wood, medicinals, and fruits. Most products are used locally within traditional societies, making it difficult to place a monetary value on their worth. Further study on bat-plant interactions is needed to determine the extent to which the region's plants depend on pteropodids for seed dispersal or pollination.

Many species of flying foxes are threatened by destruction of their habitat, overexploitation for human food, and extermination as agricultural pests (Wiles and Payne 1986; Heaney and Heideman 1987; Pierson and Rainey 1992; Wiles 1992; Fujita and Tuttle, unpublished manuscript). Unfortunately, conservation efforts are hampered by public misconceptions about bats and a basic lack of information on their distribution, abundance, and ecology.

The ecological importance of flying foxes as seed dispersers and pollinators for a vast number of paleotropical plant species is only now being recognized (Fujita and Tuttle, unpublished manuscript). However, these services also have important economic ramifications that may directly affect local and world markets. Comparatively little is known of bat-plant interactions or their economic significance on Pacific islands. In this paper, we list the known food plants of pteropodids in the region, and we present information on products derived from these plants that are used by humans. We hope that this summary will help to stimulate further research on bat-plant interactions and their economic significance and to strengthen arguments for the conservation of flying foxes in Oceania.

We have limited this review geographically to include the islands in Micronesia northward to the Ogasawara Islands and those in the southern Pacific from the Solomons to New Caledonia and eastward. Eight genera and about 36 species of flying

foxes occur in this region (Nowak and Paradiso 1983), including about 23 species of *Pteropus*, 4 of *Nyctimene*, 3 of *Pteralopex*, 2 of *Melonycteris*, and a single species of *Dobsonia*, *Macroglossus*, *Notopteris*, and *Rousettus*.

Methods

We reviewed the zoological and botanical literature to identify the food plants of flying foxes in the tropical Pacific region. Only feeding observations that identified plants primarily to species level were taken from these references. A similar literature review was conducted to determine products derived from these plants and the extent of their use, both in trade and for noncommercial purposes (Safford 1905; Wilder 1931; Chistopherson 1935, 1938; Yuncker 1943; Degener 1949; Stone 1963, 1970; Sykes 1970; Haddock 1974; McMakin 1975; Lessa 1977; Moore and McMakin 1979). The plant taxonomy used in this paper largely follows Fosberg et al. (1979, 1987) and Smith (1979, 1981, 1985, 1988). We have updated a number of plant names from those given in the original references to reflect current taxonomic nomenclature.

Results

Bat Food Plants

Information on the food habits of flying foxes was obtained for 13 species of bats from 16 Pacific island groups (Table). However, of these, dietary information is reasonably extensive for only two species of *Pteropus* in several localities. These are *P. mariannus* in the Mariana Islands (Safford 1905, 1910; G. J. Wiles, personal observation; P. O. Glass, U.S. Fish and Wildlife Service, Houston, Texas, personal communication; E. M. Taisacan, Division of Fish and Wildlife, Department of Natural Resources, Rota, CNMI, personal communication) and Yap (Falanruw 1988), and *P. tonganus* in Niue (Wodzicki and Felten 1975) and the Cook Islands (Wodzicki and Felten 1980). Data on foods are lacking or anecdotal for the remaining pteropodid species in the region.

In general, fruit and flower resources from a broad range of plants are eaten. Our list of bat foods contains 69 genera and 84 species of plants, including 4 species identified to genus only, from 41 plant families (Table). Plant families most strongly represented were Myrtaceae, Moraceae, Anacardiaceae, Leguminosae, and Pandanaceae. The plant parts consumed included the fruits of 65 species, the flowers of 35 species, the leaves of 5 species, and the sap of 1 species (Table). Dietary diversity in a single species of flying fox in one island group is best exemplified by *P. mariannus* in the Marianas, where 39 species of plants are known to be visited.

Flying foxes are attracted to many of the same species or genera of plants on different islands throughout the region. Taxa that are commonly selected include *Artocarpus*, *Carica papaya*, *Ceiba pentandra*, *Cocos nucifera*, *Eugenia*, *Ficus*, *Freycinetia*, *Inocarpus fagifer*, *Mangifera indica*, *Musa*, *Pandanus tectorius*, *Syzygium*, and *Terminalia catappa* (Table). Interestingly, many of these plants are cultivated by islanders or grow semiwild near human habitations. The predominance of species associated with people is probably related to several factors, among which are that humans and flying foxes share similar taste preferences in fruits (Marshall 1983; Tidemann and Nelson 1987) and that observers are more likely to encounter bats foraging near towns, villages, and family farming plots. Records of pteropodids feeding on native forest plants in the Pacific are much more limited and are probably greatly underrepresented in the literature.

Like pteropodids in other parts of the world (Marshall 1983), *Pteropus* on Pacific islands have been successful at exploiting a number of introduced plants as food sources that also attract bats in their native ranges. These include paleotropical species such as *Artocarpus altilis*, *Cananga odorata*, *Eugenia javanica*, *E. malaccensis*, *Mangifera indica*, some *Musa*, and some *Syzygium*, and neotropical plants such as *Agave*, *Annona*, *Carica papaya*, *Ceiba pentandra*, *Cestrum diurnum*, *Persea americana*, and *Psidium guajava* (Table).

Products from Bat Plants

A thorough analysis of the products obtained from bat-visited plants in Oceania is hindered by a sparse ethnobotanical literature, particularly for Melanesia and Fiji. Several of the references used here were based on field studies conducted before 1960; some of the recorded uses of plants may no longer be widely practiced as some island societies become increasingly modernized. With these limitations in mind, we documented a variety of products that are derived from plants that depend to varying degrees on flying foxes for seed dispersal

Table. *Known food plants of* Pteropus *and other flying foxes in the tropical Pacific region. Products that islanders derive from these plants are listed only for the island groups where this information is known.*

Plant	Bat	Food[a]	Location	References[b]	Products[c]
Agavaceae					
Agave americana	*Pteropus pselaphon*	fl	Ogasawara, Iwo	9	
Agave rigida	*Pteropus mariannus*	fl	Marianas	20	ornamental
Anacardiaceae					
Campnosperma brevipetiolata	*Pteropus mariannus*	fr	Yap	6	
Dracontomelon sp.	*Pteropus tonganus*	fr	Vanuatu	2	
Mangifera indica	*Pteropus mariannus*	fr	Marianas	22	fruits eaten; sap used medicinally[c]
	Pteropus mariannus	fr	Palau	23	fruits eaten
	Pteropus mariannus	fr	Yap	6	fruits eaten
	Pteropus ornatus	fr	New Caledonia	19	
	Pteropus tonganus	fr	Cooks	26	fruits eaten
	Pteropus tonganus	fr	Niue	25	
	Pteropus tonganus	fr	Samoa	3	fruits eaten
Semecarpus atra	*Pteropus ornatus*	fr	New Caledonia	19	seeds eaten
Semecarpus venenosus	*Pteropus mariannus*	fr	Yap	6	
Spondias dulcis	*Pteropus* sp.	fr	Samoa	21	fruits eaten
Annonaceae					
Annona muricata	*Pteropus mariannus*	fr	Yap	6	fruits eaten
Annona reticulata	*Pteropus mariannus*	fr	Marianas	16	fruits eaten[c]
Cananga odorata	*Pteropus samoensis*	fl	Samoa	5	wood used to build canoes; flowers used to make leis and scent coconut oil
	Pteropus tonganus	fr	Cooks	26	flowers used in garlands and to scent coconut oil
	Pteropus tonganus	fl	Samoa	5	
Apocynaceae					
Cerbera manghas	*Pteropus tonganus*	fr	Cooks	26	fruits and flowers used medicinally
Neisosperma oppositifolia	*Pteropus mariannus*	fr	Marianas	22	wood used for furniture[c]
	Pteropus mariannus	fr	Palau	23	
	Pteropus mariannus	fr	Ulithi	24	seeds eaten rarely; wood used for canoes, houses, and firewood; medicinal uses
	Pteropus tonganus	fr	Niue	25	wood used for houses and weapons[c]; branches carved into nose flutes
Ochrosia mariannensis	*Pteropus mariannus*	fr	Marianas	22	
Araliaceae					
Osmoxylon mariannensis	*Pteropus mariannus*	fr	Marianas	20	
Arecaceae (Palmae)					
Clinostigma ponapensis	*Pteropus molossinus*	fr	Pohnpei	10	
Cocos nucifera	*Pteralopex atrata*	fr	Solomons	18	numerous uses among Pacific islanders (see text)
	Pteropus insularis	fl	Chuuk (Truk)	22	
	Pteropus mahaganus	fr	Solomons	18	
	Pteropus mariannus	fl	Marianas	22	
	Pteropus mariannus	sap	Ulithi	24	
	Pteropus mariannus	?	Yap	6	
	Pteropus molossinus	fl	Pohnpei	22	
	Pteropus ornatus	fl	New Caledonia	19	
	Pteropus tonganus	fl	Cooks	26	
	Pteropus tonganus	fl	Samoa	5	
	Pteropus woodfordi	fr, fl	Solomons	13, 18	

Table. *Continued.*

Plant	Bat	Food[a]	Location	References[b]	Products[c]
Gulubia palauensis	*Pteropus mariannus*	fl	Palau	23	
Bombacaceae					
Ceiba pentandra	*Pteropus mariannus*	fl	Marianas	7, 22	fruit fibers used as stuffing[c]
	Pteropus mariannus	fl	Yap	6	fruit fibers used as stuffing
	Pteropus molossinus	fl	Pohnpei	10	
	Pteropus samoensis	fl	Samoa	3, 5	fruit fibers used as stuffing
	Pteropus tonganus	fl	Cooks	26	fruit fibers used as stuffing
	Pteropus tonganus	fl	Niue	25	fruit fibers used as stuffing
	Pteropus tonganus	fl	Samoa	3, 5	
Caricaceae					
Carica papaya	*Pteropus mariannus*	fr	Marianas	7, 22	fruits eaten
	Pteropus mariannus	fr	Yap	6	fruits eaten
	Pteropus ornatus	fr	New Caledonia	19	
	Pteropus samoensis	fr	Samoa	3	fruits eaten; bark used medicinally
	Pteropus tonganus	fr	Cooks	26	
	Pteropus tonganus	fr	Samoa	3	
	Pteropus tonganus	fr	Vanuatu	2	
Casuarinaceae					
Casuarina equisetifolia	*Pteropus mariannus*	fl	Marianas	22	lumber; firewood
Chrysobalanaceae					
Parinari sp.	*Pteropus mariannus*	fl	Yap	6	
Combretaceae					
Terminalia catappa	*Pteropus mariannus*	fr, fl	Marianas	22	seeds eaten[c]; wood used for small utensils[c]
	Pteropus mariannus	fr	Palau	23	
	Pteropus mariannus	fr	Yap	6	seeds eaten
	Pteropus tonganus	fr	Cooks	26	wood used for domestic utensils
	Pteropus tonganus	fr	Vanuatu	2	
Lumnitzera littorea	*Pteropus mariannus*	fl	Yap	6	
Cunoniaceae					
Geissois ternata	unidentified pteropodid	fl	Fiji	8	wood used to build homes
Cycadaceae					
Cycas circinalis	*Pteropus mariannus*	fr	Marianas	22	seeds used to make flour[c]; seeds and bracts used medicinally[c]
	Pteropus mariannus	fr	Palau	23	
Ebenaceae					
Diospyros samoensis	*Pteropus tonganus*	fr	Niue	25	fruits used as a fish poison; wood used for weapons[c]
Elaeocarpaceae					
Elaeocarpus joga	*Pteropus mariannus*	fr, fl	Marianas	7, 17	lumber[c]
Elaeocarpus augustifolius	*Pteropus ornatus*	fr	New Caledonia	19	
Elaeocarpus rarotongensis	*Pteropus tonganus*	fl	Cooks	26	
Ericaceae					
Vaccinium sp.	*Pteropus anetianus*	fr	Vanuatu	1	
Euphorbiaceae					
Glochidion ramiflora	*Pteropus tonganus*	?	Vanuatu	2	
Glochidion sp.	*Pteropus mariannus*	fl	Yap	6	
Gentianaceae (Loganiaceae)					

Table. *Continued.*

Plant	Bat	Food[a]	Location	References[b]	Products[c]
Fagraea berteriana	*Pteropus mariannus*	fl	Marianas	7	
	Pteropus tonganus	fr	Cooks	26	
Guttiferae (Clusiaceae)					
Calophyllum inophyllum	*Pteropus mariannus*	fr	Marianas	22	lumber[c]
	Pteropus mariannus	fr	Ulithi	24	wood used for tools and canoes; medicinal and ceremonial uses; other minor uses
	Pteropus mariannus	fr, fl	Yap	6	
	Pteropus tonganus	fr	Samoa	5	wood used for houses, canoes, and utensils; seeds, leaves, sap, and bark used medicinally
Mammea odorata	*Pteropus mariannus*	fr, fl	Marianas	7, 22	wood used for houses[c] and as a dye[c]
Heliconiaceae					
Heliconia solomonensis	*Melonycteris woodfordi*	fl	Solomons	12	
Hernandiaceae					
Hernandia sonora	*Pteropus mariannus*	fr	Marianas	22	lumber[c]; firewood[c]; leaves, bark, and seeds used medicinally[c]
Icacinaceae					
Merrilliodendron megacarpum	*Pteropus mariannus*	fr	Marianas	20	
Lauraceae					
Persea americana	*Pteropus mariannus*	fr, fl	Marianas	7	fruits eaten
	Pteropus tonganus	fr	Cooks	26	
Lecythidaceae					
Barringtonia asiatica	*Pteropus mariannus*	fl	Marianas	7	seeds used as a fish poison[c]; fruit and bark used medicinally[c]
Leguminosae (Caesalpiniaceae and Fabaceae)					
Cynometra ramiflora	*Pteropus mariannus*	lv	Marianas	20	
Erythrina variegata	*Pteropus mariannus*	fl	Marianas	7, 22	ornamental; lumber[c]; leaves used medicinally[c]
Inocarpus fagifer	*Pteropus mariannus*	fr	Yap	6	seeds eaten
	Pteropus tonganus	fr	Cooks	26	fruits are an important food source (?[c]); seeds eaten
	Pteropus tonganus	fr	Niue	25	seeds eaten; wood used; leaves used medicinally
Intsia bijuga	*Pteropus mariannus*	fl	Palau	23	
Mucuna gigantea	*Pteropus mariannus*	fl	Marianas	7, 22	leaves used medicinally[c]
Meliaceae					
Aglaia mariannensis	*Pteropus mariannus*	fr	Marianas	22	wood used for small objects[c]
Dysoxylum moata	*Pteropus samoensis*	fr	Samoa	3	
Melastomataceae					
Melastoma denticulatum	*Pteropus* sp.	fr	Fiji	4	leaves used medicinally
Moraceae					
Artocarpus altilis	*Pteropus mariannus*	fr	Marianas	7, 22	fruits eaten; wood used for houses and canoes[c]; bark used to make cloth[c]; sap used medicinally[c], as a caulk[c], and to make paint[c]

Table. *Continued.*

Plant	Bat	Food[a]	Location	References[b]	Products[c]
	Pteropus mariannus	fr, lv	Ulithi	24	staple food; wood used for canoe parts and houses; other minor uses
	Pteropus mariannus	fr	Yap	6	staple food
	Pteropus samoensis	fr	Samoa	5	staple food; wood used for houses; fruit paste used as a caulk
	Pteropus tonganus	fr	Cooks	26	staple food
	Pteropus tonganus	fr	New Caledonia	15	
	Pteropus tonganus	fr	Niue	25	fruits eaten
	Pteropus tonganus	fr	Samoa	3, 5	
Artocarpus heterophyllus	*Pteropus mariannus*	fr	Yap	6	fruits eaten
	Pteropus tonganus	fr	Cooks	26	seeds eaten
Artocarpus mariannensis	*Pteropus mariannus*	fr, lv	Marianas	7, 22	fruits and seeds eaten;[c] lumber[c]
	Pteropus mariannus	lv	Palau	23	
Artocarpus sp.	*Pteropus tonganus*	fr	Vanuatu	1, 2	
Ficus copiosa	*Pteropus tonganus*	fr	Vanuatu	2	
Ficus prolixa	*Pteropus mariannus*	fr	Marianas	22	sap used medicinally[c]; tree is culturally significant for Chamorros
	Pteropus mariannus	fr	Ulithi	24	leaves used medicinally; aerial roots used as lashings
	Pteropus mariannus	fr	Yap	6	
	Pteropus tonganus	fr	Cooks	26	bark used to make cloth and fiber
	Pteropus tonganus	fr	Niue	25	bark used to make tapa cloth; aerial roots used as cordage
Ficus tinctoria	*Pteropus mariannus*	fr	Marianas	7	firewood[c]
Ficus sp.	*Pteropus anetianus*	fr	Vanuatu	14	
	Pteropus mariannus	fr	Marianas	7, 22	
	Pteropus mariannus	fr	Palau	23	
	Pteropus mariannus	fr	Yap	6	
	Pteropus samoensis	fr	Samoa	3	
	Pteropus tonganus	fr	Vanuatu	14	
Musaceae					
Musa nana	*Pteropus tonganus*	fr	Niue	25	fruits eaten; a minor export
Musa paradisiaca	*Pteropus tonganus*	fr	Niue	25	fruits eaten; a minor export
Musa sp.	*Notopteris macdonaldi*	fl	Vanuatu	14	fruits eaten
	Pteropus mariannus	fr	Marianas	22	fruits eaten; fruits made into flour[c]
	Pteropus mariannus	fr, fl	Ulithi	24	fruits eaten; fiber used to make cloth; medicinal uses
	Pteropus mariannus	fr	Yap	6	fruits eaten
	Pteropus ornatus	fr	New Caledonia	19	fruits eaten
	Pteropus tonganus	fr	Cooks	26	fruits eaten
	Pteropus tonganus	fr, fl	Samoa	3, 5	fruits eaten; household uses
	Pteropus tonganus	fr	Vanuatu	2	
	Pteropus sp.	fr	Samoa	21	
Myrtaceae					
Eugenia javanica	*Pteropus mariannus*	fr	Ulithi	24	wood used for canoe parts, houses, and firewood; medicinal and ceremonial uses
Eugenia malaccensis	*Pteropus mariannus*	fr	Palau	23	
	Pteropus tonganus	fr, fl	Cooks	26	fruits eaten
	Pteropus tonganus	fl	Vanuatu	14	

Table. *Continued.*

Plant	Bat	Food[a]	Location	References[b]	Products[c]
	Pteropus sp.	fr	Samoa	21	fruits eaten
Eugenia sp.	*Pteropus mariannus*	fr	Yap	6	fruits eaten
Melaleuca viridiflora	*Pteropus ornatus*	fl	New Caledonia	19	
Metrosideros villosa	*Pteropus tonganus*	fl	Tonga	11	
Psidium guajava	*Pteropus mariannus*	fr	Marianas	16	fruits eaten[c]; wood used for tools[c] and firewood[c]; fruits and leaves used medicinally[c]
	Pteropus ornatus	fr	New Caledonia	19	
	Pteropus tonganus	fr	Cooks	26	
	Pteropus tonganus	fr	Vanuatu	2	
Syzygium clusiifolium	*Pteropus tonganus*	fr, fl	Niue	25	wood used for firewood
Syzygium cumini	*Pteropus tonganus*	fr	Cooks	26	
Syzygium inophylloides	*Pteropus tonganus*	fl	Niue	25	important timber tree; wood used for firewood
Syzygium jambos	*Pteropus tonganus*	fr	Samoa	3	
Syzygium richii	*Pteropus tonganus*	fr, fl	Niue	25	important timber tree
Syzygium sp.	*Pteropus anetianus*	fr	Vanuatu	14	
	Pteropus ornatus	fr	New Caledonia	19	
	Pteropus tonganus	fr	Vanuatu	14	
Pandanaceae					
Freycinetia hombronii	*Pteropus* sp.	fr	Fiji	4	roots used to make rope
Freycinetia reineckei	*Pteropus mariannus*	fr, fl	Marianas	7, 22	stems used as lashings[c]
	Pteropus tonganus	fl	Samoa	3	
Freycinetia sp.	*Pteropus mariannus*	fl	Yap	6	
Pandanus tectorius	*Pteropus mariannus*	fr, fl	Marianas	7, 22	numerous uses among Pacific islanders (see text)
	Pteropus mariannus	fr	Palau	23	
	Pteropus mariannus	fr	Ulithi	24	
	Pteropus mariannus	fr	Yap	6	
	Pteropus tonganus	fr, fl	Cooks	26	
Pandanus sp.	*Pteropus pselaphon*	fr	Ogasawara, Iwo	1, 9	
	Pteropus tonganus	fr	Niue	25	
Passifloraceae					
Passiflora suberosa	*Pteropus mariannus*	fr	Marianas	22	
Passiflora sp.	*Pteropus ornatus*	fr	New Caledonia	19	
Piperaceae					
Macropiper puberulum	*Pteropus* sp.	fr	Fiji	4	leaves and bark used medicinally
Rubiaceae					
Guettarda speciosa	*Pteropus mariannus*	fl	Marianas	7	
	Pteropus mariannus	fr, lv	Ulithi	25	wood used for houses, paddles, and firewood; medicinal uses; flowers used in leis
Rutaceae					
Citrus sinensis	*Pteropus tonganus*	fr	Cooks	26	fruits eaten and exported
Citrus sp.	*Pteropus mariannus*	fr	Yap	6	fruits eaten
	Pteropus sp.	fr	Samoa	21	fruits eaten
Sapindaceae					
Cupaniopsis samoensis	*Pteropus samoensis*	fr	Samoa	3	
Pometia pinnata	*Pteropus tonganus*	fr	Niue	25	fruits eaten
Tristiropsis obtusangula	*Pteropus mariannus*	fr	Marianas	22	lumber[c]
Sapotaceae					
Manilkara sp.	*Pteropus pselaphon*	fr	Ogasawara, Iwo	1	
Planchonella torricellensis	*Pteropus samoensis*	fr	Samoa	5	

Table. *Continued.*

Plant	Bat	Food[a]	Location	References[b]	Products[c]
	Pteropus tonganus	fl	Niue	25	lumber
	Pteropus tonganus	fr	Samoa	5	
Solanaceae					
Cestrum diurnum	*Pteropus mariannus*	fr	Marianas	22	ornamental[c]
Solanum lycopersicum	*Pteropus tonganus*	fr	Niue	25	fruits eaten
Sonneratiaceae					
Sonneratia alba	*Pteropus mariannus*	fr,fl,lv	Yap	6	
Urticaceae					
Dendrocnide latifolia	*Pteropus mariannus*	fr	Marianas	22	
Pipturus argenteus	*Pteropus mariannus*	fr	Marianas	22	
Verbenaceae					
Premna obtusifolia	*Pteropus mariannus*	fr	Marianas	22	wood used for houses[c]; leaves used medicinally[c]

[a] Plant parts eaten include: fr: fruit; fl: flowers; lv: leaves; ?: not identified by author.

[b] References: 1. Andersen (1912); 2. Baker and Baker (1936); 3. Cox (1983); 4. Degener (1949); 5. Engbring, unpublished manuscript; 6. Falanruw (1988); 7. P. O. Glass (personal communication); 8. Guppy (1906); 9. Imaizumi (1970); 10. Jackson (1962); 11. Jaeger (1954); 12. Kress (1985); 13. Lawrence (1945); 14. Medway and Marshall (1975); 15. Ridley (1930); 16. Safford (1905); 17. Safford (1910); 18. Sanborn (1931); 19. Sanborn and Nicholson (1950); 20. E. M. Taisacan (personal communication); 21. Whitmee (1874); 22. G. J. Wiles (personal observation); 23. Wiles and Conry (1990); 24. Wiles et al. (1991); 25. Wodzicki and Felten (1975); 26. Wodzicki and Felten (1980).

[c] Denotes a plant product that is no longer widely used in the location given.

or pollination (Table). Most of these items are used locally within the region's traditional cultures. The placing of a monetary value on such products is impossible because these cultures are not strongly tied to a cash economy. We recorded 113 products; timber and other wood products (25 species), medicinals (22 species), and fruits (19 species) were the three largest categories (Table). Additional items were classified as fuels (11 species), other foods (9), cordage (4), household articles (3), fiber for cloth (3), ornamentals (3), thatching (2), fish poisons (2), personal adornments (2), and other products (8). A number of plants are used for more than one purpose, but two species, *Cocos nucifera* and *Pandanus tectorius*, are particularly valuable because of the large number of products obtained from them.

Flying foxes feed on the flowers of coconut palms (*Cocos nucifera*) on many islands (Table) and may assist in the pollination of this tree. Pacific islanders rely on this species for many vital products, including food, drink, oil, timber, thatching, mats, fuel, fiber, medicine, domestic utensils, animal fodder, and cooking ingredients (Safford 1905; Barrau 1961; Burkill 1966; Purseglove 1972; Lessa 1977). On a commercial basis, coconut products in the form of copra, coconut oil, desiccated coconut, copra meal cake, and fresh fruit are moderately valuable exports for a number of Pacific island nations. Insects and wind are reported to be the main pollinators of coconut flowers (Burkill 1966; Purseglove 1972; Opeke 1982). However, because of the sizable number of records of pteropodids visiting the flowers (Table), we speculate that the value of nocturnal pollination by flying foxes, particularly the small nectivorous species, has perhaps been overlooked.

Pandanus tectorius, and perhaps other species of *Pandanus*, may rely heavily on flying foxes to disperse its large seeds on islands where both coexist (Wiles et al. 1991). On many islands, *Pandanus* is second only to the coconut palm in terms of utility to residents. The leaves are used as thatching and in making woven mats, baskets, and bags. The fruits are edible and are an important seasonal food on some Micronesian atolls (Miller et al. 1956). Other parts of the plant are used medicinally, as fuel, and for other purposes (Stone 1963). Handicrafts made of *Pandanus* leaves are produced in limited quantities on some islands and are sold locally to tourists or exported to commercial outlets on larger islands (Stone 1963; Sykes 1970; G. J. Wiles, personal observation).

Some other bat-visited plants have the potential to become important to the economies of Pacific islands, based on the value of the same species in

other areas of the world. For example, *Sonneratia alba,* which occurs in Melanesia and the Caroline Islands, is important in the wood chipping industry in tropical Asia. *Ceiba pentandra* also produces fibers and oil that are exported from the Asian region (Fujita and Tuttle, unpublished manuscript).

Discussion

Fujita and Tuttle (unpublished manuscript) reviewed the zoological literature and documented the foods of flying foxes throughout their distribution in the Old World. They recorded more than 300 plants from 59 families that were visited by bats for fruit, nectar, or pollen. Marshall (1985) also published an extensive list of known food plants for the Megachiroptera, although his identifications were limited to the generic level. Our list of food plants for flying foxes is the most complete thus far compiled for the Pacific region, with 84 species of plants recorded.

In the paleotropics, morphological similarities, or syndromes, exist among many of the food plants of pteropodids and point to the importance of bats as seed dispersal or pollination agents. A number of species, especially those in the families Moraceae, Anacardiaceae, Annonaceae, and Sapotaceae, produce fruits that appear, because of their size, color, odor, or exposed hanging position, to be adapted for dispersal by bats (van der Pijl 1957). Other species, particularly those in the Myrtaceae, Bignoniaceae, Bombacaceae, and Sapotaceae, exhibit flower morphologies and other traits that similarly suggest a strong coadaptation between the plant and bats (Faegri and van der Pijl 1979).

In this paper, we compiled the information necessary to illustrate that flying foxes can be economically important to humans on Pacific islands. However, the existing literature for this region, as for other parts of the world, is far from complete, and we can only estimate the value of the plants serviced by pteropodids.

Most Pacific economies are based on subsistence agriculture, and in general the region has few exportable crops. Timber and coconut products are the region's most important commodities that may be ecologically linked with flying foxes. The Solomon Islands, Fiji, Vanuatu, and Western Samoa are exporters of timber to Asia; however, we were unable to determine which tree species dominate the harvest or whether any of these are visited by bats. One quarter of the world's copra comes from the Pacific, and on some islands, such as Pohnpei and Tonga, copra is the largest export item. Between 1986 and 1988, the annual income received from exported coconut products averaged U.S. $8.7 million for Western Samoa, $6.6 million for Vanuatu, $5.3 million for the Solomons, and $2.9 million for Fiji (Food and Agricultural Organization 1990). Handicrafts woven from *Pandanus* or carved from certain woods are another (much smaller) revenue earner that may be linked to bats.

Fujita and Tuttle (unpublished manuscript) identified a number of plant products that are more directly linked with flying foxes elsewhere and are commercially valuable in world markets. Mangrove species in the genus *Sonneratia,* which occur from coastal Southeast Asia to eastern Australia, are bat pollinated and are important in paper and wood chipping industries. Other bat-visited trees are among the most important timber species of the countries in which they occur, providing millions of dollars annually in exports. These include the Coromandel ebony (Ebenaceae: *Diospyros melanoxylon*), the Bornean mahagony (Guttiferae: *Calophyllum inophyllum*), several species of *Palaquium* (Sapotaceae) from Southeast Asia, the African iroko tree (Moraceae: *Chlorophora excelsa*), the Australian black bean (Leguminosae: *Castenospermum australe*), and at least nine species of Australian *Eucalyptus* (Myrtaceae; Dalziel 1937; Burkill 1966; Purseglove 1968; Boland et al. 1984).

Other plants serviced by pteropodids produce fruits that are exceptionally valuable as domestic and export products. In Southeast Asia, the durian (Bombacaceae: *Durio zibethinus*) has been estimated to be worth U.S. $120 million annually in regional sales (Myers 1985). The durian market is now also expanding to the west and can be found in New York, Los Angeles, and Honolulu (M. S. Fujita, personal observation). In Malaysia, Indonesia, and especially Thailand, durian is increasingly cultivated on plantations, in addition to the harvesting of fruits from wild plants (M. S. Fujita, personal observation). All of these trees require natural pollinating agents, the most important of which are smaller flying foxes, to set fruit and maintain outcrossing (Soepadmo and Eow 1976).

Bananas, perhaps the most important fruit in the world, originated in Southeast Asia (Purseglove 1972). Only two species, *Musa nana* and *M. paradisiaca,* are cultivated on a large scale in the tropics, including most Pacific nations, for local use or as an export. Both of these domestic

varieties no longer depend on bats for pollination in order to set fruit because they are seedless and vegetatively propagated. However, most of the approximately 20 species of wild bananas still depend on pteropodids for pollination (Nur 1976). Wild species are important in maintaining the genetic vigor of domestic varieties. Thus, preservation of the wild ancestors and their pollinators is necessary to ensure the health and productivity of cultivars.

In the Pacific, where subsistence lifestyles are still prevalent, and the remainder of the paleotropics, most items derived from plants serviced by flying foxes are important primarily on a village or regional level (Fujita and Tuttle, unpublished manuscript). Many products are not necessarily sold in marketplaces or tied to a cash economy, and determination of their monetary value is difficult. This is particularly true for the medicinal uses that were documented. About 20% of the products recorded in both studies were used as folk medicines.

Other examples of locally valuable products from Southeast Asia include the midnight horror tree (Bignoniaceae: *Oroxylum indicum*), which is used as a food, a medicinal, and to produce a black dye for coloring rattan baskets (Burkill 1966; van Steenis 1977); and petai (Leguminosae: *Parkia speciosa* and *P. javanica*), which has garlic-flavored seeds used to spice curries and other local dishes (Burkill 1966; M. S. Fujita, personal observation). Each of these species depends on pteropodid bats for pollination (Start 1974; Start and Marshall 1976; Gould 1978). Ng (1980) estimated that domestic sales of petai in peninsular Malaysia alone at almost U.S. $15 million per year, illustrating that such products can be a significant part of a region's economy.

On Pacific islands, pteropodid bats can also be considered to be economically important in that they are integral to the maintenance of the unique and lush rainforests that attract tourists to the region. Further, flying foxes themselves may have economic value as a tourist attraction (Wiles and Payne 1986). For example, the diurnal Samoan flying fox (*Pteropus samoensis*) is a highlighted feature of a newly legislated national park in American Samoa (Anonymous 1988).

Our information from Oceania suggests that many of the plants serviced by flying foxes produce products useful to humans. More research on bat-plant interactions is needed to ascertain the full extent to which the region's economically and ecologically important plant species depend on pteropodid bats for seed dispersal or pollination. These data are especially needed in the Pacific, where endemism among plants and animals may be high and interactions more tightly coupled than in ecosystems with more diverse floras and faunas on larger land masses.

The economic role of flying foxes is only beginning to be recognized. Nevertheless, flying foxes are threatened by overhunting and habitat loss in many of the same areas that benefit from their interactions with plants. Public awareness campaigns that promote flying fox conservation are urgently needed to avert future extinctions of some species. To be effective such programs must point out that these bats are economically more valuable as seed dispersers and pollinators of island flora than they are as a food item. This argument can also be used to convince government officials of the need to establish protective legislation for flying foxes.

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The Cultural Significance of the Flying Fox in Samoa: A Legendary View

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Long before the arrival of the first Samoans several thousand years ago, bats were the sole terrestrial residents on our island. In a sense, humans have been their guests for more than three millennia. In Samoa the flying fox has always been an integral part of both the physical and cultural landscape. Thus, the flying fox soars along the ridges and through the plantations of our history and consciousness.

To appreciate the cultural role played by flying foxes in history, look at the earliest cultural record of these fascinating creatures. In an ancient society like Samoa, oral tradition of cultural expression still predominates. Early records reside largely in oral narratives, such as legend and mythology. The question then arises: How best to access and interpret such information in a manner that reflects the cultural matrix from which it arose in the first place? This essay offers a folkloristic perspective that addresses the relation between oral lore and cultural reality. The discipline of anthropological folklore examines traditional oral and material cultures of a people in order to better understand what those people hold significant. One unusual aspect of folklore is that its analytic methods can be focused on most aspects of a society, including bats.

For example, one of the best known Samoan legends about the flying fox is the story of Leutogitupa'itea, a Samoan maiden in distress:

> Leutogi was married to the Tuitoga, the King of Tonga. The king had two wives—Leutogi, who was Samoan, and another, who was Tongan. After some time the Tongan wife had a child, but Leutogi remained childless. Her jealousy over the Tongan wife's new status was increased because the Tongan wife constantly teased her about it. As a result, Leutogi spent much time alone in the woods, and when the king and his friends planned to hunt flying foxes she would warn the bats in order to spite her husband. Thus, the flying foxes came to recognize the unhappy Leutogi as their friend.
>
> After a time, Leutogi resolved to get rid of the child. One day the wives went together to their bathing place, and the Tongan wife asked Leutogi to hold the child while she bathed first. As soon as her rival was out of sight, Leutogi seized the moment to kill the infant. The Tongan wife, hearing the sudden wild cry of her child, returned, but the baby was already dead. When the king heard of this evil deed, he became so angry that he ordered that Leutogi be burned alive.
>
> The unlucky woman was dragged by his men into the bush and bound in the fork of a *fetau* tree. Soon a tall heap of dry wood surrounded her. Then the people set fire to it, and, not wishing to hear Leutogi's screams, they returned to the village. But as soon as the flames began to rise, something truly extraordinary took place—thousands of flying foxes came out of the jungle and extinguished the fire by urinating on it.
>
> When the king's attendants returned, they found Leutogi still alive and the fire out. They were very surprised and hurried back to tell the king what had happened. Next, Tuitoga ordered that Leutogi be taken and abandoned on a barren, uninhabited island. This island was haunted by a demon named Losi, and the king, who knew this, was certain that Losi would soon kill Leutogi. Losi, however, did not touch her because he thought she would soon die for want of food and water. So he simply sat down to wait and watch her die.

Great, therefore, was Losi's surprise when the next day he saw a multitude of flying foxes, each bringing some kind of food to Leutogi. The bats continued in this way to feed her for days as Losi looked on, amazed.

After some time, the Fijian Tuiuaea happened to sail close to that island. Leutogi called out to him and begged him to take her along with him. This he did gladly, and, as she was a very good looking woman, he married her and in due time she bore him a son (Henry 1983; Fitisemanu n.d.).

We streamlined the legend somewhat in this version. The narrative is still significant because the content of such stories suggests underlying beliefs, social understandings, and historical contexts. For example, two central motifs are in this tale that are truly exceptional in Polynesian legend—a protagonist saved by urination and also saved by airlifted food.

Investigators in any discipline compile and study masses of data, looking for the patterns that are the field context and for the exceptions to those patterns that offer the communicative content. To a folklorist these two unique Polynesian motifs signal that something special is happening here, and the agent in both instances is the flying fox.

In both of these significant motifs the message is that flying foxes are indigenously associated with fertility and fecundity. The second motif is the more obvious: A barren, uninhabitable, demon-infested island is made viable through the agency of flying foxes; the monster of starvation is defeated. The first motif delves more deeply into the erotic subconscious, but it directly associates flying foxes with fertility and survival. In a fuller version of the legend, Leutogi, still tied in the *fetau* tree after the bats have extinguished the fire, says to the Tuitoga's men words that live on as a Samoan proverb: "*Ua tatou fetaia'i i le magafetau soifua*"—"We meet under the *fetau* tree while yet full of life" (Henry 1983).

In fact, a simplistic version of this association of the flying fox with rain lives on in a Samoan children's song still sung today, similar to our American nursery rhyme, "Rain rain go away":

Le pe'a, le pe'a e, amo tele lau 'avega
'Aua ne'i timu se'i matou eva
Tifitifi e tagi loa laofie.

Flying fox, flying fox, take your burden far away
Don't rain, so we can play
Tifitifi, cry immediately the rain stops
(Moyle 1988).

To a folklorist, another feature of this legend is its associations of liminality. Liminality is a term coined and elaborated on by anthropologists Arnold Van Gennep and Victor Turner to describe the state of being "in-between" categories, marginal, anomalous, "neither fish nor fowl." Leutogi, for example, the hero of this tale, is a liminal person—a Samoan woman in a Tongan household, which, incidentally, reflects the reality of a historical period when Samoa was to some extent subjugated by neighboring Tonga. She befriends and is befriended by a liminal species, the flying fox, which while mammalian, and thus able to urinate effectively, also flies, unlike other mammals. Such overlapping categories of existence often occupy a unique and significant niche in the worldview of indigenous people (Mary Douglas 1966). Often, as in the case of Leutogi and her bat-saviors, liminality connotes a kind of supernatural sanction exerting its influence on human affairs from some Olympian vantage point. To the folklorist, such liminal characters found in traditional lore signal something significant going on in the cultural belief system, which expresses itself metaphorically through legend and mythology.

Samoa is the eastern boundary of the flying fox's natural habitat, but strangely enough, it is not the eastern boundary of Polynesian lore about giant bats. Great, often man-eating, bats are found in Hawaiian, Maori, and Tuamotuan traditions (Grace 1907; Stimson 1937; Beckwith 1940). Hawaiian legend even includes an eight-eyed bat (Thrum 1923; Beckwith 1940). It is interesting that giant bat stories have persisted in these "flying-fox-less" societies, which evolved from western Polynesian cultures where flying foxes had been prevalent.

It is in flying fox country, however, western Polynesia—Samoa, Tonga, Niue, Fiji, and the outliers—where the most integrated flying fox traditions are encountered. We find bats as gods in both Tikopian and Tongan myths (Collocott 1921; Gifford 1924), and in Fijian lore a giant white vampire bat acts as a messenger (Fison 1904).

In a rather complex Niuean narrative about a war between the birds and the beasts, we again encounter the flying fox's inherent liminality. Here the bat's nocturnal and aloof habits are explained as a result of its being scorned by both the birds

and the beasts because during the mythic war the flying fox played politics, switching from side to side as the fortunes of war waxed and waned, dealing upon its double nature (Loeb 1926). And in Tikopian legend we have the Polynesian prototype for Bruce Wayne (Batman), a creature who is sometimes bat and other times man (Firth 1961).

But what do such local legends and myths contribute to our understanding of the contemporary cultural significance of the flying fox? A series of recent interviews with Samoans in Samoa revealed a continuity between traditional and contemporary attitudes toward flying foxes. Most striking of these is that flying foxes still occupy a liminal position in the Samoan view of nature. While the *pe'a* is identified and appreciated as an integral and highly valued part of the traditional Samoan forest, during fruit harvesting season it may be viewed as a pest as it competes with farmers for the fruit crop.

A traditional story about a rat tricking a bat out of his wings (Kramer 1902) is still told and reveals this ambivalence. Also, the most common method of hunting flying foxes before the arrival of fire arms indicates a type of pest control. The barbed branches of a creeper vine were tied to a handle, and the hunter would try to hook the bat, tearing its wings, as it fed upon flowering banana plants in the plantation (Hiroa 1930).

Although their flesh is still prized as a delicacy, it is not considered "feast food," and the selling of flying foxes is almost universally frowned on. We have never seen flying foxes for sale in Samoa, either in the farmers' markets or elsewhere. The actions of individuals in recent years to harvest and export Samoan flying foxes are commonly seen as criminal activities—greedy and shameful behavior. The flying fox has never been a staple of the Samoan diet. Most often when it is taken, the one or two bats are offered to elders or other ranking family members as an in-group delicacy gift.

Our survey revealed the vast majority of Samoans questioned support recent efforts to protect the *pe'a vao* (*Pteropus samoensis*) and *pe'a faitaulaga* (*Pteropus tonganus*). Older Samoans are shocked by the dwindling number of flying foxes, and in both American and Western Samoa villagers respect local restrictions on bat hunting. The general attitude is that the flying fox is a part of the forest, a part of Samoa; and while limited hunting of flying foxes should still be allowed, care must be taken to preserve them for future generations.

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Part 2.

Population Threats

Small Islands, Natural Catastrophes, and Rapidly Disappearing Forests: A High Vulnerability Recipe for Island Populations of Flying Foxes

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Introduction

In number of species, geographic range, and population sizes flying foxes have been the most successful group of native mammals to colonize the islands of the Pacific (Rainey and Pierson 1992). Unlike Pacific island birds, bats did not suffer mass extinctions during the pre-European period, though they were hunted by native islanders (Dye and Steadman 1990). Unfortunately, a record of extinctions and population declines in many species has marked the last 20 years of flying fox history in the region (Ralph and Sakai 1979; Wodzicki 1981; Wiles and Payne 1986; Falanruw 1988; Flannery 1989; Wiles et al. 1989). Not surprisingly, habitat destruction and overharvesting for subsistence and commerce are the culprits in most instances (Cox 1983; Wiles and Payne 1986; Wiles et al. 1989). However, simply knowing what caused these declines does not yield obvious solutions because both hunting and habitat destruction are likely to continue for some time.

The best option, under such dynamic circumstances, is to develop management strategies based on the population biology of each species (Gilpin 1989), and—particularly in the case of flying foxes—to ensure these strategies are especially sensitive to the structure and dynamics of the species' habitat and the catastrophic events it encounters regularly (Gilpin 1987, 1989). Completing this task optimally would require a thorough knowledge of the population biology of each of the 55 species that occur on the Pacific islands (Rainey and Pierson 1992). Unfortunately, neither detailed nor long-term biological studies have been conducted on even a single species. The basic biology of most species is poorly known.

Falanruw (1988) and Pierson and Rainey (1992) summarized the biological information on island populations of flying foxes. In general, flying foxes are relatively large for an island mammal, and they reproduce slowly, each female producing only one young per year. Most species are social, some living in small groups, while others form large, highly interactive groups consisting of thousands of individuals. Roost sites are usually in large trees or, in the case of a few species, coastal mangrove forests. They often forage in groups for fruits, seeds, pollen, or nectar in highland and lowland forests, but the latter habitat type is preferred by most species. Knowledge of the population biology and demographics of flying foxes is at even a more rudimentary stage. Only recently have formal censuses been conducted on a few species (Wiles et al. 1989), and then usually only on one or a few populations of a species.

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My focus is on the role habitat structure, habitat dynamics, and catastrophes play in determining the vulnerability of flying foxes. The habitat on which flying foxes depend is naturally divided into small, often scattered blocks and, as a consequence, many flying fox populations are often small, scattered, and isolated (Rainey and Pierson 1992). This population structure itself poses special problems (Franklin 1980; Soulé 1980). Some of the habitat blocks are shrinking or disappearing because of deforestation, and superimposed upon this dynamic are catastrophic factors (typhoons and volcanic eruptions) that frequently take place. My purposes are to evaluate the significance of small island size, deforestation, and catastrophic events to flying foxes, and to present management guidelines derived from demographically similar species that could be used for flying foxes until sufficient population data can be obtained.

Small Islands

The Pacific land region consists of about 25,000 islands, most of them very small. From an ecological perspective, a judgment about an island's size depends on the size of the organism in question because a small organism can maintain a large population on a small island, provided that most of the island is suitable habitat. I would contend that flying foxes are large relative to the size of many of the islands they inhabit. This contention is supported by the fact that flying fox population sizes on small islands do not exceed several hundred, even when they appear to be near carrying capacity (Wiles et al. 1989). The idea that a population size of 200–300 is small is a judgment drawn from population genetics and relates to the ability of a population to respond to selective pressures over time (Soulé 1987).

In addition to occupying small islands, Rainey and Pierson (1992) have shown that most flying foxes have restricted distributions. Thirty-eight of the 55 island species occupy land areas of less than 50,000 km^2, and 22 live on less than 10,000 km^2.

Generally, when populations are under similar environmental pressures (e.g., predators and competitors) their numbers tend to be proportional to the size and quality of the available habitat (Wilcox 1980). Formal census data for one species of flying fox supports that generalization (Wiles et al. 1989), and the same observation has been made, informally, many times. Thus, at the upper limit flying fox populations are restricted primarily by island size and the amount of suitable habitat on each island.

Typhoons, volcanic eruptions, deforestation, and hunting are factors that distort the normal relation between island size and the population size of flying foxes (Wiles et al. 1989). The first two factors strike islands of all sizes without prejudice, but the two human-related factors affect large islands more often than small ones. This is simply because large islands are more likely to be inhabited by humans. Human-related deforestation on large islands tends to be focused on lowland areas (Marten 1985), the preferred habitat for many flying foxes. Thus, the largest blocks of habitat—the ones most likely to support the greatest number of flying foxes—are being selectively removed or made uninhabitable. The result for any single species is a smaller total number of individuals divided up into smaller population units. It may also mean greater fragmentation and the occupation of suboptimal habitats.

The significance of this conversion to a set of smaller population sizes is that, in general, the probability of extinction is inversely correlated with population size (Kepler and Scott 1985). The larger the system the lower the extinction rate, and evidence shows that the relation is nonlinear (Ims and Stenseth 1989). In the Ims and Stenseth study, a two-fold increase in population space produced a six-fold increase in the mean time to extinction.

Natural Catastrophes: Typhoons and Volcanic Eruptions

The effects of typhoons on flying foxes have been observed on numerous occasions and are both direct and indirect (Flannery 1989; Bani 1992; Craig and Syron 1992; Lemke 1992). Some animals are killed outright, and the potential for substantial losses is high during the reproductive season. Often, forests are almost completely leveled, destroying roost trees and food sources. If alternative habitat is unavailable, the survivors starve. Following storm-related deforestation, flying fox camps become much more conspicuous, and hunters have been observed taking advantage of the bats increased vulnerability (Stinson et al. 1992).

Typhoons are not rare events. Bani (1992) stated that typhoons commonly strike Vanuatu,

and Craig and Syron (1992) estimated a major storm hits Samoa every 3 years. The frequent references to typhoons in the rather sparse flying fox literature supports the conclusion that they are regular events. Given the rather long average life span of these animals (Pierson and Rainey 1992), one would estimate an individual flying fox would experience two or three typhoons during its life span.

The potential for serious negative effects from typhoons is magnified when a population is small or the population (or species) is restricted to a single island or a close-knit group of islands. Under this combination of circumstances the probability of extinction increases greatly (Shaffer 1987). This probability becomes particularly alarming when one notes that 35 of the 55 species occur on a single island or a group of small islands (Rainey and Pierson 1992), and that deforestation and hunting are shrinking the population sizes and ranges of most species.

Because volcanic activity is restricted to a relatively small number of islands and is unlikely to cause much direct mortality, it is normally less significant to flying foxes than are typhoons. However, volcanic activity in some island chains has restricted the amount of habitat available to flying foxes in that region (Wiles et al. 1989; Lemke 1992).

Deforestation

Survival of flying foxes is directly dependent on the persistence of island forests, which provide them with most of their food and roost sites. The equation is simple, the more forest there is, the more flying foxes there are likely to be. As discussed in the previous section, deforestation from storms and volcanic eruptions can be significant, but it is magnitudes less important than human driven deforestation. Stinson et al. (1992) reported deforestation rates exceeding 95% on Tinian and Saipan, and there are reports of high deforestation rates throughout the Pacific island region (Cox 1983; Marten 1985). On many Pacific islands, deforestation has been an ongoing phenomenon for centuries (Reader 1988), but the rate has greatly accelerated during the last 20 years because of human population growth and commercial logging (Marten 1985; Richardson 1985). Marten (1985) estimated that the inhabited islands will be completely deforested within 20 years if the present trends continue.

Unfortunately, humans and flying foxes have similar tastes in islands and habitats. Flying foxes have their largest populations on the largest islands, and most prefer lowland forests; these areas are also the favored locations of farmers, agroforesters, loggers, and developers. Consequently, some species are able to survive only on small, isolated islands (Wiles et al. 1989). For some species, mangrove forests are critical roost areas, and they are being destroyed at a rapid rate for the woodchip industry.

The largest and best flying fox habitat was probably destroyed centuries ago, and the populations that exist today are the remnants of once larger assemblages.

Consequences and Actions

Typhoons, volcanic eruptions and associated deforestation, and populations scattered over small islands have always been factors in the lives of flying foxes. Until recently, they fared amazingly well under those circumstances, despite their low reproductive rates. Their successes have been caused, in part, by their ability to move between neighboring islands, a rather broad diet, a lack of predators on many islands, and social habits. Recently, the formula has changed because flying fox populations are smaller, more fragmented, or restricted to single islands or a small group of islands, and in some cases, suffer higher predation from introduced animals (Wiles et al. 1989). Consequently, natural catastrophes that were once of little long-term consequence suddenly become important because flying foxes are more vulnerable as a result of their modified population structures (Gilpin 1987, 1989).

Preliminary recommendations are necessary before adequate data are available for those species already thought to be in danger of extinction or reduced to a point of ecological insignificance. Wildlife managers would like to know what the minimum viable population (MVP) size is for the species of flying foxes they manage. However, it would be exceedingly difficult to calculate a reliable MVP figure for any species until more data are available (Soulé 1986, 1987). Five-hundred is the figure most often associated with the term MVP, but this particular number comes from a long-term study done on grizzly bears (Shaffer 1983) and is likely to be inappropriate for flying foxes (Soulé 1986, 1987; Gilpin 1989).

In the absence of adequate population data about flying foxes, a practical strategy might be to examine the data from better-studied mammals of roughly similar size, social habits, and reproductive biology. Critical measures and criteria gleaned from these studies could be applied to flying fox populations until more appropriate population data can be gathered. Primates are the only mammal group similar to flying foxes and for which sufficient population data are available.

Dobson and Lyles (1989) recently reviewed the literature for the primates and reached the following conclusions. First, the more social and sexually promiscuous the species the lower the population density at which the species can maintain itself. Monogamous and somewhat less social species would be at the greatest risk and least able to recover from drastic population reductions. Second, populations collapse when the survival of adult females falls below 70% per interbirth interval. For flying foxes this would translate to a maximum death rate of 30% of the adult females per year from all causes. Third, populations were extremely sensitive to variations in recruitment. A similar point made by Goodman (1987) and Redford and Robinson (1989) states that the probability of extinction goes up with increases in population variations over either time or space. Any factor that had an appreciable effect on recruitment rate had a disproportionate affect on population size and stability. For example, a species may be distributed over a number of habitat patches, but one or two of those patches may be much better than others during the breeding season. Destruction of those one or two patches would have a disproportionately negative effect on the population.

Like flying foxes, primates are subject to considerable human harvest pressure, and Dobson and Lyles (1989) pointed out that unless harvests are routinely monitored and regulated they are likely to result in population collapse, as the case has been with many fisheries. Pierson and Rainey (1992) demonstrated at current harvest levels one of the Samoan flying foxes could be driven to extinction within a decade. Their model does not take into account catastrophic factors such as the typhoon that struck the island in March 1990. Dobson and Lyles also emphasized that without good data on recruitment (and recruitment rates vary over both time and space), it is impossible to determine safe harvest levels. In fact, the prospects for managing even well-studied species with the combination of life history traits of flying foxes and primates are poor.

Conclusions

The past success of flying foxes proves that they are well adapted to dealing with the biological problems associated with living on small islands that are subject to the catastrophic weather and geological events that often destroy portions of their habitat. The ability of flying foxes to prosper under those natural conditions depended on low mortality rates, populations scattered over many islands, and substantial amounts of alternative habitat. The combination of hunting, especially for market, and habitat losses, primarily from deforestation, cast against the difficult biological norm for these species, is a recipe for disaster. Experiences with primates serve as a strong warning that flying foxes are likely to be highly vulnerable to extinction. Therefore, management strategies should err toward the conservative in order to preserve these animals. Assessing a population's status with a minimum of data stands as the most urgent problem facing biologists attempting to conserve and manage flying fox populations.

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Conservation and Subsistence Harvesting of Pacific Island Flying Foxes

by

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Introduction

Throughout the earth's recent history, humans have had to perform a balancing act—consume enough resources to meet daily needs but leave enough for tomorrow. There is no place on our planet where the failure to achieve this balance is more obvious than on oceanic islands. For instance, since the arrival of humans in eastern Polynesia, more species of landbirds have become extinct than survive there today (Steadman 1989). Many of these extinct birds were megapodes, rails, and pigeons (Balouet and Olson 1989) that disappeared less than 2,000 years ago coincident with the appearance of man. This pattern, coupled with the large size of the birds, indicates that human hunting led to the avian extinctions. Other factors, such as small population sizes and geographic isolation, also contribute to the high extinction rates on islands (Robertson 1992).

Population reductions and extinctions of insular species continue unabated and are not restricted to birds. Populations of flying foxes, or fruit bats, have been reduced by overhunting on many islands in the Indian (Racey 1979; Cheke and Dahl 1981) and Pacific Oceans. The little Marianas flying fox, *Pteropus tokudae*, was endemic to Guam but is now extinct (Wiles 1987). The large Palau flying fox, *Pteropus pilosus*, has not been observed this century and is thought to be extinct (Wiles and Payne 1986). Overhunting on Guam has reduced the once large population of the Marianas flying fox, *Pteropus mariannus*, to less than 600 individuals (Wiles 1987). These bats are considered a delicacy by Chamorro residents of Guam and are served at a variety of social functions. As the local populations of bats declined, Guamanians began importing flying foxes from other Pacific islands, and the hunting became commercialized. The consequences of this commercialization and trade have been severe and are reviewed by Wiles (1992).

Although commercial hunting has been the major problem for Pacific bats, hunting for local consumption has also caused extinctions and reduced bat populations. *Dobsonia chapmani* and *Aproteles bulmerae* have apparently disappeared from the Philippines and Papua New Guinea due at least in part to overharvesting (Heaney and Heideman 1987; Flannery 1990). In the Cook and Niue Islands, declining populations of the Tongan flying fox, *Pteropus tonganus*, are probably the result of overhunting (Wodzicki and Felten 1975, 1980). On the island of Lekeba in Fiji, bats were annually herded to one end of the island and then clubbed and eaten (Kay 1986). Flying foxes are hunted for local consumption in the more remote areas of Samoa (Cox 1983) and on Yap and Tonga (Falanruw 1988). The diets of people in Indonesia (Fujita 1988), Irian Jaya (Craven 1988), and Vanuatu (Anonymous 1988) also include flying foxes.

The overharvesting of bats on Guam illustrates how unregulated subsistence hunting for flying foxes can lead to substantial population declines and to commercialized hunting, which can extirpate island populations. Thus, hunting, even for local consumption, needs to be regulated in order to manage flying fox populations so they remain large enough to be functional in the rain forest ecosystems.

This paper offers suggestions that may help prevent the overharvesting of flying foxes that frequently occurs when noncommercial hunting becomes commercialized. I will develop operational definitions for subsistence hunting, discuss how the threat from noncommercialized hunting changes with modernization, and present recommendations concerning management of flying fox populations.

What is Subsistence Hunting?

There are several factors that make it difficult to rigorously define the term "subsistence hunting." For instance, some people use the term "subsistence" interchangeably with the term "traditional." Others use the terms to describe distinctly different harvests. Another difficulty is that subsistence and commercial activities lie along the same activity continuum, and to draw a line separating the two requires making an arbitrary judgment.

There are several legal definitions available for "subsistence." The Alaska Lands Conservation Act (Section 803) defines the term as follows:

> "subsistence uses" means the customary and traditional uses by rural Alaska residents of wild, renewable resources for direct personal, or family consumption as food, shelter, fuel, clothing, tools, or transportation; for the making and selling of handicraft articles out of nonedible by-products of fish and wildlife resources taken for personal or family consumption; for barter, or sharing for personal or family consumption; and for customary trade.

Application of this definition to flying foxes is not appropriate because the definition does not distinguish among the activities that differentially influence bat populations, including subsistence hunting, hunting to provide for ceremonies, control hunting, and recreational hunting. These activities can collectively be referred to as noncommercialized hunting.

I restrict the term "subsistence hunting" to those activities that provide for basic food needs without surplus. The emphasis is on the consumption of bats for food. Subsistence hunting has probably occurred on each island that has flying foxes and continues today on many islands. This contrasts with "recreational hunting," where bats are hunted strictly for sport or enjoyment. Because recreational hunting seemingly occurs at low levels on most islands, it probably does not pose much of a population threat, unless people shoot at bats while they are roosting.

Subsistence and recreational hunting differ from "ceremonial hunting," in which bats are hunted to provide food for special cultural events. In other words, the consumption of the bats is more or less independent of the dietary needs of the people. Consuming bats at ceremonies has taken place on Guam, Saipan (Wiles and Payne 1986; Wiles 1987; Wiles et al. 1989), Yap, and Tonga (Falanruw 1988).

Control hunting involves the taking of bats because they are either consuming or perceived to be consuming produce, such as breadfruit (*Artocarpus altilis*). In the majority of cases where flying foxes eat commercial fruit, they do so when the fruit is ripe or overripe, which means the damage is usually minor for most commercial fruit growers. Individual "basket farmers" may, however, endure enough crop loss to warrant removing the bats consuming the produce.

Threats from Noncommercial Hunting

Before the appearance of modern weapons and economies, noncommercial hunting activities probably did not seriously threaten most island populations (Cox 1983; Falanruw 1988). However, as islands became modernized, many flying fox populations suffered serious population declines. The relation between time, modernization, and the threat to bat populations can be illustrated conceptually (Figure). From historic to contemporary time, weapons changed from thorn bushes to guns, economies changed from barter to cash systems, and transportation changed from simple methods and roads to efficient interisland air transport and complex roads that penetrate interior habitats.

Traditional limitations to noncommercial harvesting of bats involves restricting the consumption to certain parts of the human population, such as the less powerful groups on Yap and only the royal families on Guam and Tonga (Falanruw 1988). Harvesting flying foxes also involves considerable ritual and organization. Unfortunately, the traditional limitations on the exploitation of bats have long been forgotten on most of the islands (Falanruw 1988). Different islands, and parts of

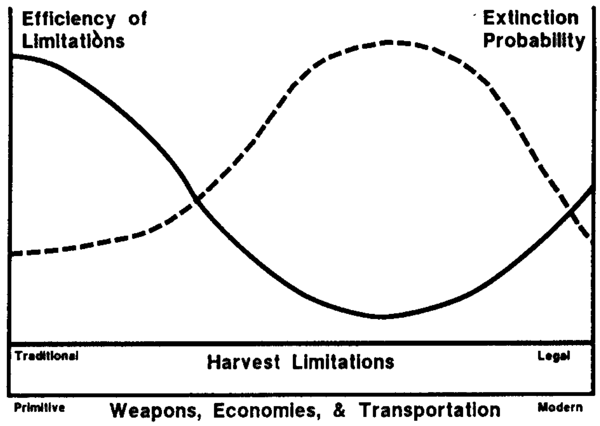

Figure. Conceptual model of how harvest limitations change with modernization. The *solid line* represents how effective the limitations are at protecting bat populations and the *dashed line* indicates the probability that flying foxes could go extinct. Horizontal axes are superimposed on a time-line from historic to contemporary time.

islands, will become modernized at different rates. Commercialization increases the rate traditional patterns of exploitation are lost, and thus the vulnerability of the populations.

At the other end of the continuum are laws created to limit the harvest of bats. A period usually exists between traditional and legal forms of limitations when there are no limitations to the harvesting of bats. This period frequently coincides with the expansion of modern weapons, transportation, and economies, placing the populations in double jeopardy. As the legal restraints become effective, however, the probability the flying fox population will become extinct is reduced.

Management Recommendations

Legal restraints include hunting regulations ranging from no hunting at all to hunting with certain conditions. The following is a list of hunting recommendations that could be used in the development of local hunting laws:

1. ban all commercial hunting,
2. prohibit any export of flying foxes,
3. prohibit shooting at or near roosts,
4. prohibit hunting during the daytime,
5. prohibit hunting during the birthing and weaning seasons,
6. establish a daily bag limit,
7. establish a possession limit, and
8. establish a plan to control excessive harvesting of flying foxes following a natural catastrophe.

The first two recommendations are designed to prevent the overharvesting driven by commercialization and trade with Guam. Ideally, no export of flying foxes should be allowed, including those labeled as personal, in order to make controlling exports feasible. Personal exports create a loophole in the trade regulations that has been exploited to support the Guam market for flying foxes.

Hundreds of bats can be killed with just a few shots at a colony. Thus, the shooting of weapons should not be allowed at bat colonies or within a kilometer of these colonies. This will reduce the probability of a massive slaughter of bats and the chances shooting will disturb the colony, causing it to relocate. Most species of flying foxes (except *Pteropus samoensis*) roost during the day. Thus, daytime shooting for bats would most likely be conducted at the roosting area, an activity that should be strictly prohibited.

Flying foxes have a low reproductive rate with long gestation and weaning periods (Falanruw 1988). The populations are most vulnerable during the birthing and weaning periods. Hunting should be prohibited during these times to maintain population levels. Control hunting should be restricted to the taking of bats as they are consuming produce. Farmers should not be allowed to take any bat they simply assume is consuming produce, or to shoot bats at any colonies.

Finally, limits to the number of bats that can be taken should be established. In the absence of valid data on population levels and recruitment, a daily bag limit of five or fewer individuals is suggested. A possession limit of double the daily limit should also be established so hunters do not become involved with commercialized hunting. A season limit of no more than double the possession limit should also be considered for the same reason. Regulations such as these should apply to all four types of noncommercialized hunting in order to make it easier for people to comply. Separate regulations for each category would be impossible to enforce.

Conclusion

Unregulated hunting of flying fox populations can reduce their numbers to dangerously low levels and cause extinctions. Consequently, island lead-

ers, legislators, and wildlife managers have the responsibility to regulate hunting so the flying foxes can continue to pollinate flowers and disperse seeds at the rain forest ecosystem level. If hunting is allowed, research should be given high priority in order to obtain the data necessary to manage bat populations. Suggested management and research objectives are outlined in the appendix. Successful implementation of hunting regulations, and ultimately the conservation of island flying foxes, will depend on carefully planned education programs that emphasize the local importance of flying foxes and the need to conserve them.

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Appendix. Outline for a Pacific Island Flying Fox Research and Management Plan[1]

1. Determine the status and distribution of flying foxes.
   a. Conduct periodic surveys of the abundance and distribution of flying foxes.
   b. Continue to gather information on roosting bats.
   c. Improve survey techniques.
2. Determine reproduction and recruitment rates of flying fox populations.
3. Control illegal hunting of flying foxes.
   a. Regularly patrol public and private lands for bat poaching.
   b. Continue to monitor illegal hunting activities.
   c. Interview former hunters to learn more about hunting techniques.
   d. Prosecute flying fox poachers.
   e. Involve Police Department in law enforcement efforts.
4. Determine habitat and dietary requirements of flying foxes.
   a. Conduct field studies to determine geographical areas occupied.
   b. Develop detailed descriptions of occupied habitats and map these areas.
   c. Determine the minimum area of suitable habitat needed to sustain a viable population of bats.
   d. Gather field data on use of foods.
   e. Determine the phenology of bat foods.
   f. Determine movement patterns of flying foxes.
5. Legally protect and manage essential forest ecosystems.
   a. Provide maximum legal protection to essential forest habitats of flying foxes on public and private lands.
   b. Limit human-related disturbances in essential habitats.
      1. Prohibit forest clearing in essential habitats.
      2. Prohibit hunting near known flying fox colonies.
   c. Maintain buffer zones of vegetation surrounding essential habitat of flying foxes.
   d. Determine the impact of introduced species on essential habitats and take corrective action if necessary.
   e. Establish plantings of food trees for flying foxes.
6. Develop an education program (Morton 1990).
7. Augment existing populations by reintroducing flying foxes to suitable habitat within their former ranges.
   a. Determine the proper time to start a reintroduction program.
   b. Determine the sources of bats for a reintroduction program.
   c. Determine the number and location of sites for reintroduction and provisions to protect and monitor them.
   d. Determine whether a protective breeding program can produce flying foxes for release.

[1] Modified from USFWS recovery plan Wiles (in press).

Part 3.

Population Status

Recent Trends in the Fruit Bat Trade on Guam

by

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Abstract. Residents of Guam have imported large numbers of fruit bats (*Pteropus* spp.) from other Pacific islands during the last 20 years as a food item. The quantity of bats shipped to the island peaked in the late 1970's, when approximately 20,000–29,000 bats were imported annually. Since 1981, imports have declined to an estimated mean of 13,150 bats per year. During the 1970's, importers acquired bats mainly from the Caroline Islands (Palau and Yap) and other islands in the Marianas (primarily Saipan, Rota, and Tinian). During the mid-1980's, the market shifted; most bats came from Western Samoa, Palau, American Samoa, Tonga, Papua New Guinea, and the Philippines. Since 1987, Palau, Pohnpei, and Chuuk have been primary sources of imported bats. An estimated 66–83% of all imported bats are sold commercially after arriving on the island. The recent inclusion of seven species of *Pteropus* on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) is expected to provide adequate protection for most populations of these fruit bats, once enforcement occurs. However, greater exploitation of populations of *P. mariannus* in Palau and the Mariana Islands and of some species listed in Appendix II will probably result.

A number of populations of Pacific island fruit bats currently are threatened by overhunting for export to Guam and the Commonwealth of the Northern Mariana Islands (CNMI), where many Chamorro residents enjoy eating bats as a traditional food. Fruit bats, primarily of the genus *Pteropus*, have been imported to Guam from a number of Pacific islands and several Asian countries during the last 20 years (Payne 1986; Wiles and Payne 1986; Wiles 1987a). The bat trade on Guam seems to have begun in the 1960's, when the number of Marianas fruit bats (*P. mariannus*) on the island was declining rapidly because of severe overhunting (Perez 1972; Wiles 1987b). By 1974, the population of these bats fell to less than a hundred animals (Wiles 1987b). The population now numbers about 600 bats, which is too low to allow hunting by local residents. A second species of *Pteropus*, the little Marianas fruit bat (*P. tokudae*), also occurred on Guam, but is now believed to be extinct as of the late 1960's or 1970's for reasons unknown. The decline in the availability of local bats caused Guam residents to acquire bats from neighboring islands.

In this paper, I describe the import trade in fruit bats on Guam and summarize the origins and volumes of bats shipped to the island during the last 15 years. I also provide new information on imports from 1985 to 1989 to update previous reports on the trade (Payne 1986; Wiles and Payne 1986; Wiles 1987a).

Data Collection

The importation of fruit bats to Guam is now controlled only by the Guam Department of Agriculture, which has issued import permits for this activity since 1975. Current import procedures are similar to those described by Wiles and Payne

(1986). Import permits and certificates of origin are mandatory for all shipments of bats entering the island. The department upholds the Federal Lacey Act and requires that imported bats be harvested according to the laws of the exporting island.

Several explanations account for the difficulty in collecting exact import data (Payne 1986; Wiles and Payne 1986). In most cases, customs officials rely on importers to provide the number of bats contained in shipments. However, in large shipments, fruit bat carcasses are often frozen together in blocks, making verification of numbers impossible for inspectors. A few entry permits are occasionally lost enroute to wildlife officials and are never tabulated.

Smuggling fruit bats into Guam is another problem reported to exist, but difficult to confirm and quantify. Customs inspections improved substantially since 1983, and officers are more proficient now at recording actual shipment sizes on entry documents. Before then, inspections were less stringent and the correct number of bats in shipments often went unrecorded by officers. When this occurred, wildlife officials recorded the number of bats requested for import on the permit, a figure that can be much larger than the actual number of animals imported. Because of that practice, import figures for the late 1970's and 1980 may be somewhat inflated. The import statistics I provide have been corrected of a few minor errors that were published in the annual reports of the Guam Division of Aquatic and Wildlife Resources and in Payne (1986), Wiles and Payne (1986), and Wiles (1987a).

Results

Excluding 1977, when data were not collected, an estimated total of almost 221,000 fruit bats were imported to Guam between 1975 and 1989 (Table 1). Importations were highest during the late 1970's, when 20,000 to 29,000 bats were brought in annually (Fig. 1). Since then, imports have decreased to 9,400–16,700 bats per year, with fluctuations in volume common between years. A total of almost 16,700 bats in 1989 is the largest number of bats to enter the island in a single year since 1980.

In the 1970's and early 1980's, most fruit bats shipped to Guam originated from the Caroline Islands, primarily Palau, and other Mariana Islands (Fig. 2). Between 1983 and 1986, the market shifted so islands and countries outside of Micronesia, particularly Western Samoa, were the primary sources of bats brought to Guam. This change mainly resulted from the efforts of a single merchant from Guam, who cornered much of the commercial market for bats during this period. He regularly traveled to Western Samoa, American Samoa, the Philippines, Tonga, and Papua New Guinea, and he actively sought out business contacts who were willing to export bats. After his business failed in late 1986, many people returned to acquiring their bats from the nearby and more convenient islands of Palau, Pohnpei, and Chuuk. Recent changes in laws that prohibit exports of bats from Western and American Samoa also probably have contributed to the shift back to bats from the Carolines.

Records of the number of fruit bat shipments to enter Guam have been kept since 1982. They reveal an almost eight-fold increase in shipments between 1983 and 1989 (Table 2). There was a significant decrease, however, in the mean number of bats contained in shipments. Average shipment size between 1987 and 1989 was 45.2 bats.

Commonwealth of the Northern Mariana Islands

The Commonwealth of the Northern Mariana Islands (CNMI), which includes the islands of Saipan, Tinian, Rota, and Pagan, was an important source of imported fruit bats for residents of Guam during the early years of the trade (Wiles and Payne 1986). Between 1975 and 1981, the annual volume of imports varied from about 1,950 to 3,850 animals per year (Table 1). Shipments ceased in early 1982 after Guam passed its own Endangered Species Act, which prohibited the importation of all *P. mariannus mariannus* from other islands (Wiles and Payne 1986). This law protects the population of *P. m. mariannus* on Guam in two ways: (1) it removes the threat that locally taken bats could be sold illegally among bats of the same subspecies from neighboring islands, and (2) it reduces hunting pressure on bats on other Mariana Islands, particularly Rota. Recent evidence of interisland movements indicates all fruit bats in the southern Marianas belong to one contiguous population, and currently, the population of bats on Guam is probably being maintained by immigration of animals from Rota (Wiles and Glass 1990). Minimum population estimates of *P. mariannus* in the Marianas were provided by Wiles et al. (1989).

Table 1. *Numbers of fruit bats imported to Guam by fiscal year from 1975*–1989. Most data lacking for 1977.

	1975	1976[a]	1977	1978[a]	1979	1980[a,b]	1981[c]	1982	1983	1984	1985	1986	1987	1988	1989	Total
American Samoa	0	0	—	0	0	540	500	40	30	1,632	853	525	0	0	35	4,155
Commonwealth of the Northern Mariana Islands																
Rota	1,893	1,655	—	1,225	732	552	700	366	0	0	0	7	14	1	0	7,145
Saipan	76	1,841	—	1,050	1,822	1,603	1,100	150	0	0	91	54	5	6	15	7,813
Tinian	50	159	—	433	343	231	150	0	0	0	0	0	0	0	0	1,366
Pagan	0	190	—	0	0	0	0	0	0	0	0	0	0	0	0	190
Federated States of Micronesia																
Chuuk	0	0	—	67	0	76	300	207	0	0	37	739	646	1,216	2,507	5,795
Kosrae	0	0	—	0	0	27	0	0	0	27	0	0	0	0	15	69
Pohnpei	0	254	—	0	221	3,925	500	366	310	344	458	204	1,075	1,088	6,478	15,223
Ulithi	0	0	—	0	0	13	0	0	0	0	0	0	0	0	37	50
Yap	865	3,284	—	4,515	2,896	8,790	3,000	0	0	0	0	0	17	15	28	23,410
Fiji	0	0	—	0	0	6	0	0	0	0	0	0	0	0	0	6
Indonesia	0	0	—	0	0	0	0	0	0	0	0	7TO	0	0	7	
Palau	5,304	12,896	—	12,374	18,606	13,791	8,250	6,764	1,105	4,025	1,458	2,402	7,092	10,585	7,532	112,184
Papua New Guinea	0	0	200	0	0	0	0	0	50	1,539	0	0	0	0	0	1,789
Philippines	0	0	—	0	0	0	0	200	0	0	0T2,57II71		150	0	3,092	
Solomons	0	0	—	0	1	0	0	0	0	0	0	0	0	0	0	1
Tonga	0	0	—	0	0	0	0	0	3,050	2,030	0	0	0	0	0	5,080
Vanuatu	0	0	—	0	0	0	0	0	0	12	0	0	0	0	0	12
Western Samoa	0	0	—	0	0	0	750	2,700	8,350	6,649	7,187	6,945	300	460	0	33,341
Unknown	0	0	—	0	0	0	0	0	0	0	0	4	84	66	17	171
Total	8,188	20,279	(200)	19,664	24,621	29,554	15,250	10,793	12,895	16,258	10,084	13,458	9,404	13,587	16,664	220,899

[a] Figures for 1976, 1978, and 1980 are extrapolations based on data collected for periods of 8–11 months.
[b] Figures for 1980 cover a 15-month period.
[c] Import data were not tabulated in 1981 but were extrapolated using the number of requests and the request-import ratio for each island group in 1980, 1982, and 1983.

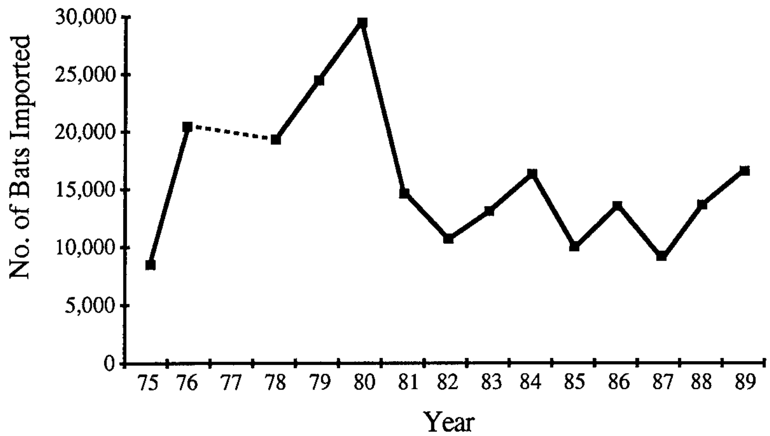

Fig. 1. Annual number of fruit bats imported to Guam from other Pacific islands from 1975 to 1989. Data are not available for 1977. Data for 1980 cover a 15-month period.

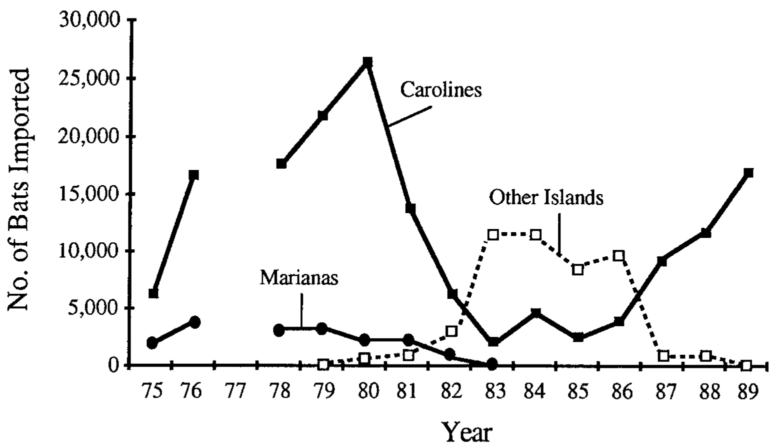

Fig. 2. Annual number of fruit bats imported to Guam from islands in the Marianas, the Carolines, and from outside of Micronesia between 1975 and 1989. Data are not available for 1977. Data for 1980 cover a 15-month period.

Table 2. *Annual number of fruit bat shipments imported to Guam and average number of bats contained in each shipment, 1982–1989.*

Year	Number of shipments received	Average number of bats imported per shipment
1982	136	79.4
1983	45	286.6
1984	97	167.6
1985	83	121.5
1986	134	100.4
1987	215	43.7
1988	317	42.9
1989	345	48.3

Since 1985, an average of about 40 fruit bats per year has been imported annually from the CNMI (Table 1). Shipments of these bats were illegal under the Guam Endangered Species Act, and all shipments were confiscated by customs authorities on Guam. The shipments included small numbers of *P. m. mariannus* and a few transhipped bats of other taxa, including *P. vampyrus* from the Philippines and *P. m. pelewensis* from Palau, that buyers had purchased on Saipan and tried to bring back with them to Guam.

Palau

Palau has shipped about 112,000 fruit bats to Guam since 1975 (excluding 1977), making it the largest single supplier of bats for the island (Table 1). The volume of exports was highest from 1976 to 1980, but decreased from 1983 to 1986, when the market in bats from Western Samoa opened up. Since 1987, the level of exports has increased again, ranging from about 7,100 to 10,600 bats per year. Between 1987 and 1989, an average of 207 shipments of bats per year entered Guam from Palau.

Biologists examined about 50 shipments of Palau fruit bats, containing more than 400 animals, confiscated on Guam between 1984 and 1989. All of the bats in these shipments were

tentatively identified as *P. mariannus pelewensis*; no *P. pilosus* were found. This provides further evidence of the probable extinction of *P. pilosus*, which was endemic to Palau, but which has not been recorded since the 1870's.

No population surveys of *Pteropus* have been conducted in Palau. Between 1983 and 1986, when exports were reduced, bats seemed to be more numerous than during the late 1970's (J. Engbring, U.S. Fish and Wildlife Service, Honolulu, Hawaii, personal communication). Despite the high current levels of harvest, bats are still commonly seen in some parts of the island group.

Yap

Guam received about 23,410 fruit bats from Yap between 1975 and 1981 (excluding 1977), making it the second largest exporter of bats to Guam during this period (Table 1). The government of Yap passed a law giving *P. mariannus yapensis* full protection in 1981, after overhunting reduced the remaining population to as few as 1,000 animals (M. V. C. Falanruw, as cited by Wiles and Payne 1986; Falanruw 1988a, 1988b). Surveys conducted in 1984 and 1986 revealed numbers had increased to an estimated 2,500–5,000 bats (J. Engbring, unpublished manuscripts).

Since 1987, six shipments with 60 fruit bats were confiscated upon entry into Guam. Several larger shipments of bats were possibly smuggled to Palau, and subsequently shipped to Guam with Palauan certificates of origin (M.C. Falanruw, U.S. Forest Service, Colonia, Yap, personal communication).

In November 1988, a month-long hunting season was held on Ulithi Atoll. Thirty-seven bats in two shipments were brought to Guam after the hunt. In 1986, the population of *P. mariannus ulithiensis* on the atoll was estimated to be 1,100–1,300 animals (Falanruw 1988a; Wiles, Engbring, and Falanruw, unpublished manuscript).

Chuuk (Truk)

Few fruit bats were exported from Chuuk, formerly known as Truk, to Guam through 1985 (Table 1). Volume has sharply increased since then, with a total of about 5,100 bats shipped from the island group between 1986 and 1989. About half of these exports occurred in 1989. Most of the harvested bats are believed to be *P. insularis* taken on islands in the Chuuk Lagoon, but smaller numbers of *P. phaeocephalus* and perhaps *P. molossinus* from the Mortlock Islands have also been included. The current status of *Pteropus* in the Mortlocks is not known.

Informal counts conducted in 1989 suggest fruit bat numbers decreased on the capital island of Moen and perhaps on several other large islands in the lagoon (W. E. Rainey and E. D. Pierson, Berkeley, California, personal communication). Reports from government officials concur with these observations and implicate overhunting as the cause of the decline (I. Mikel, Department of Resources and Development, Moen, Chuuk, personal communication).

Pohnpei

From 1976 to 1986, exports of fruit bats from Pohnpei to Guam were low except in 1980, when about 3,900 fruit bats were shipped from the island (Table 1). Exports increased to about 1,100 bats per year in 1987 and 1988, then swelled to almost 6,500 bats in 1989, when Pohnpei came close to surpassing Palau as the major supplier of bats for the Guam market. During 1989, the Economic Development Authority, an agency of the government of Pohnpei, acted as a wholesale marketer of fruit bats. The authority purchases bats from hunters and sells them to exporters. This is seemingly done to encourage harvesting of the island's natural resources for economic purposes. Population surveys of *P. molossinus* in Pohnpei have not yet been conducted, and there are no data to show what effects the current heavy harvest is having on the population.

Kosrae

Only three shipments totalling 69 fruit bats are documented as having entered Guam from Kosrae since 1975 (Table 1). Reliable reports from officials and visitors indicate, however, a significant illicit trade in *P. mariannus ualanus* occurred during the past several years, with all bats presumably going to the Marianas. Wiles and Payne (1986) reported similar evidence of bats being smuggled off the island in the early 1980's. The government of Kosrae has never placed any restrictions on the harvest or export of fruit bats; thus, the smuggling of fruit bats is puzzling. In 1989, government officials in Kosrae reported a general decline in the numbers of bats seen on the island (G. Jackson, Department of Conservation and Development, Lelu, Kosrae, personal communication).

Western Samoa and American Samoa

Western Samoa was the main supplier of fruit bats (*P. tonganus* and *P. samoensis*) to Guam between 1983 and 1986, with about 6,650–8,350 bats exported each year (Table 1). Exports declined to a few hundred animals per year in 1987 and 1988 after the major importer of Samoan bats for Guam went out of business. Overall, an estimated 33,000 animals were shipped to Guam between 1981 and 1988. Western Samoa passed legislation in 1989 that prohibited all further exports of bats.

Guam imported about 4,600 fruit bats from American Samoa between 1980 and 1986, with about a third of these received in 1984 (Table 1). A ban on the export of bats was established by the American Samoa government in 1986.

Wilson and Engbring (1992) described the abundance of both species of *Pteropus* in Western Samoa and American Samoa. Evidence suggests each species declined when exports to the Marianas were greatest (E. D. Pierson and W. E. Rainey, personal communication). *Pteropus tonganus* was the predominant species involved in the trade, with much smaller but unknown numbers of *P. samoensis* also included. An illegal shipment confiscated on Guam in 1989 contained 33 *P. tonganus* and 2 *P. samoensis*.

Tonga

Tonga was a major supplier of fruit bats for Guam only in 1983 and 1984, when a total of about 5,000 *P. tonganus* were exported (Table 1). No further trade has occurred since then. Little current information is available on the abundance of *P. tonganus* in Tonga.

Philippines

The Philippines have eight species of *Pteropus* and *Acerodon* (Nowak and Paradiso 1983). About 2,500 fruit bats were sent to Guam in 1986, the only year in which significant exports took place (Table 1). Species composition of the bats taken to Guam was not well documented, but identifications were made on the animals contained in several small confiscated shipments, including 20 *Pteropus vampyrus* in four shipments, 18 *Pteropus hypomelanus* in one shipment, and 1 *Acerodon jubatus* in one shipment. The Philippine government stopped issuing export permits for fruit bats in 1988 (A. R. Ballesfin, Department of Environment and Natural Resources, Quezon City, Philippines, personal communication). Many species of Megachiroptera in the Philippines have declined significantly during recent decades because of deforestation and overhunting for local use (Heaney and Heideman 1987).

Papua New Guinea

About 11 species of *Pteropus* occur within the political boundaries of Papua New Guinea (Nowak and Paradiso 1983). Large numbers of fruit bats were shipped to Guam only in 1984, when about 1,500 bats were exported (Table 1). *Pteropus macrotis* was identified as the species present in one shipment from that year. No exports to Guam have occurred since 1984. The government of Papua New Guinea has denied all export permits for fruit bats for several years (G. Kula, Department of Environment and Conservation, Boroko, Papua New Guinea, personal communication). Quantitative data are lacking on the population sizes of all *Pteropus* in the country.

Other Countries

The Guam Department of Agriculture has issued import permits for fruit bats from several other countries since 1985, including Indonesia (2,510 bats requested), Thailand (700 bats), the Cook Islands (100 bats), and Okinawa (36 bats). Of these, only one shipment of seven bats from Indonesia in 1986 actually entered Guam.

Marketing of Fruit Bats on Guam

Most fruit bats are believed to be sold after they are imported to the island, with a smaller portion brought in only for personal use. An estimate of the volume of bats sold commercially in 1989 was obtained by examining the number of bats contained in various size classes of shipments reaching the island. Shipments with ≤25 bats were considered imported for personal use, while those that contained >50 bats were probably sold by the importer. In making this estimate, I assumed half of the fruit bats imported in shipments of 26–50 animals were sold. Of the 345 shipments to Guam in 1989, 53% contained ≤25 bats, whereas only 26% held >50 bats (Fig. 3). In contrast, about two-thirds of all bats were imported in shipments of >50 animals. These bats, plus half of those from the size class with 26–50 bats, provide a total estimate of 77% of all animals being sold after entering the island. This estimate is similar to the percentage of bats sold commercially from 1983 to 1986, when about

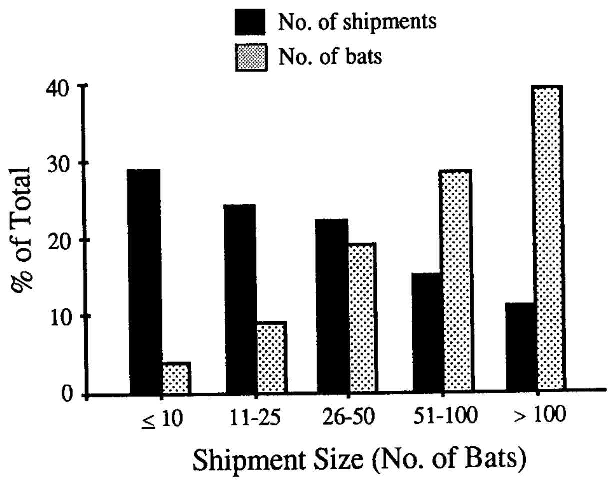

Fig. 3. Percent of fruit bats imported to Guam according to five size classes of shipments, and the percent of shipments in each size class during 1989.

66–83% of all imported bats were marketed by one of two major vendors.

Fruit bats are sold at a variety of outlets on Guam, including small grocery stores, roadside vendors, the homes of importers, and occasionally large supermarkets. No single retailer currently dominates the market, as occurred in the mid-1980's. Most retailers do not maintain steady supplies of bats. Merchants prefer instead, to sell them on an intermittent basis that is dependent on the availability of animals from wholesalers.

In 1989, retail prices of fruit bats on Guam varied from $12 to 14 per animal for *P. insularis* and *P. molossinus* to $16 to 18 per animal for *P. m. pelewensis*. Considering the small size of these taxa, retail prices have doubled to tripled on a unit weight basis since 1984 (Wiles and Payne 1986). Fruit bats can be purchased from stores or hunters on their islands of origin for $5–6 each in Palau, $4–4.75 in Pohnpei, and $3–5 in Chuuk.

Discussion

Recent changes in the fruit bat trade on Guam resulted from the business failure (for reasons unrelated to the bat trade) of the island's major retailer of bats in late 1986. This merchant marketed the vast majority of bats brought to Guam from 1982 to 1986, all of which came from islands outside of Micronesia after 1982. He typically imported bats in allotments of 100–500 animals. In 1987, his departure opened the way for a number of other small business people to enter the market. Usually, these individuals have obtained their bats from the neighboring Caroline Islands rather than from more distant sources. During this period, the number of shipments to the island increased tremendously, and average shipment size decreased. There has been an influx in small shipments of 5–20 bats, which people acquire for personal use during their travels.

The current exploitation of *P. molossinus, P. phaeocephalus,* and *P. insularis* is interesting because these are among the smallest species in the genus, weighing 100–200 g. Until recently, Guamanians often expressed a dislike for eating small fruit bats, preferring instead other taxa (such as *P. tonganus, P. samoensis, P. m. yapensis,* and *P. m. pelewensis*) that were similar in size to the larger *P. m. mariannus*, which weighs 330–620 g. The reluctance to eat small bats seems to have faded quickly as imports of some of the larger species ended.

A smaller but thriving market for imported fruit bats exists in the CNMI (Stinson et al. 1992), where resident populations of bats have dwindled during recent decades because of overhunting for local use and export to Guam (Lemke 1986; Wiles et al. 1989). To compensate for the shortage of locally harvested bats, Chamorro residents of the CNMI resorted to purchasing bats from other islands. Bat imports to the CNMI generally originated from the same islands as those coming to Guam, although in 1988 and 1989 a significant number of bats was illegally exported from Yap to Saipan (Stinson et al. 1992). Overall, imports to the Marianas totalled 19,179 bats in 1988 and 20,752 bats in 1989.

Concern about the size of the fruit bat trade in the Pacific region resulted in the listing of nine species of *Pteropus* on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1987. Seven of these species were upgraded to Appendix I in 1989, with the rest of the genus placed on Appendix II. As of March 1990, however, there was no enforcement of CITES regulations on Guam or in the CNMI. The U.S. Fish and Wildlife Service stationed a wildlife inspector on Guam in April 1990 to rectify this problem. This action will stop all further traffic in fruit bats listed on Appendix I, except for the population of *P. m. pelewensis* in Palau. This island group remains part of the Trust Territory of the Pacific Islands, which is administered by the United States. Commerce between Palau and the Mariana Islands is therefore consid-

ered as domestic trade within the United States and cannot be regulated under CITES.

Although the implementation of CITES regulations is expected to protect a number of *Pteropus* populations, several adverse effects could result, including a greater exploitation of *P. m. pelewensis* in Palau, increased illegal hunting of *P. mariannus* in the Mariana Islands, and perhaps efforts by some importers to begin smuggling bats. Bat populations may be exploited in new locations, such as Indonesia, the Solomon Islands, Vanuatu, and New Caledonia, which do not have conservation laws protecting fruit bats. It is vital customs and wildlife agencies conduct strict inspections within their jurisdictions to prevent abuses in the system.

Immediate conservation needs for fruit bats in Micronesia include the establishment of protective laws to limit or prohibit hunting in the Federated States of Micronesia and Palau, and the censusing of bat populations on these islands. Conservation education programs are needed throughout the region, especially in the Mariana Islands, where efforts to convince citizens to voluntarily reduce or end their consumption of fruit bats may be successful.

In anticipation of the increased harvesting of fruit bats in Palau, natural resource agencies in Guam and the CNMI have initiated negotiations with the government of Palau to establish an annual quota on the number of bats exported to the Marianas. The agencies hope a quota will increase protection for bats in Palau and provide the citizens of the Mariana Islands with a long-term legal, although limited, supply of bats for eating.

Acknowledgments

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Declines and Trade in Fruit Bats on Saipan, Tinian, Aguijan, and Rota

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Introduction

History

The fruit bat (*Pteropus mariannus*) has been hunted by Mariana Island natives (Chamorros) for more than 1,500 years (Butler 1988). Before European contact in 1521, Chamorro populations on individual islands reached as high as 20,000 (Farrel 1989). Bat populations may have been periodically reduced or locally extirpated, but primitive harvest methods and cultural restrictions possibly buffered the effects of hunting. Fruit bats are considered a delicacy and are usually reserved for special occasions.

In the 17th century, human populations in the Marianas declined, but large numbers of feral cattle, pigs, and goats destroyed forest habitats on some islands. Habitat destruction was most severe on Tinian, where pigs were abundant and the cattle population was estimated at 10,000 (Barrat 1988). In 1742, Tinian had extensive short pastures and forest tracts without undergrowth (Barrat 1988). Although the feral cattle had been reduced to 600–700 by 1901, pigs were still "inexhaustible" and most of the island was described as savannah (Fritz 1901). During the German administration (1899–1914), bats were the most popular game animal. Bats were hunted with guns and were said to be common on all islands (Fritz 1904). Guns were strictly controlled during the Japanese mandate (1914–44), but extensive cultivation of sugar cane severely reduced forest habitat. A post war study estimated native forest to be reduced to 2% on Tinian, 5% on Saipan, 25% on Rota, and perhaps 20% on Aguijan (Bowers 1950).

Commercial Exploitation and Declines

Little information exists about bat populations before 1979. While on Tinian, Marshall (1945) noted 500 bats in a banyan tree (*Ficus* sp.) and another colony of 50–100. Tinian may have had a bat population of several hundred to perhaps a few thousand, and Saipan up to several thousand. Guns became more readily available after World War II and unrestricted hunting occurred. A potential refuge for bats was lost when secret CIA training ceased in 1962 and the U.S. military relinquished

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exclusive use of the north end of Saipan and allowed civilian access shortly thereafter (Wootten 1984; N. Deleon Guerrero, CNMI-Department of Natural Resources, personal communication). The growing Chamorro population of Guam brought about a serious decline in fruit bat numbers there in the 1960's and early 1970's, and Commonwealth of the Northern Mariana Islands (CNMI) became a source of bats for Guam (Wiles and Payne 1986). Commercial exploitation was largely responsible for the export of over 15,000 bats between 1975 and 1981 (Wiles and Payne 1986). Little population data are available for the period, but clearly, bats were overharvested. Wheeler (1980) recorded only two bats on Tinian (21 h) and none on Saipan (22 h) in 1979. Wheeler (1980) estimated a population of only 26-109 bats on Tinian, and he thought bats may have been extirpated from Saipan. A moratorium was declared in 1977, but exports continued until 1981, when the species was protected by the Guam Endangered Species Act. Although legal exports had stopped, poaching of bats for local consumption continued (Wiles et al. 1989).

The CNMI Division of Fish and Wildlife was created in 1982, but wildlife laws were new, unpopular, and unenforced. Political and family pressures continue to be an obstacle for effective enforcement (Wiles et al. 1989). Conservation must be understood and supported by the public and elected officials before enforcement will be effective.

We describe the present status of fruit bat populations on Saipan, Tinian, Aguijan, and Rota based on survey data and incidental reports. We also analyze bat import data and discuss the CNMI as a market for other Pacific fruit bats.

Study Area and Methods

Islands included in our study were Saipan, Tinian, Aguijan (Aguiguan), and Rota, which are the southernmost islands of the CNMI. Saipan, the largest island, lies about 2,390 km SSE of Tokyo and 2,900 km east of Manila. These islands are of volcanic origin, but their surfaces are primarily uplifted limestone deposits. The human population of Saipan increased rapidly from 14,550 in 1980, to about 40,000 in 1990. Tinian has a population of about 1,500 and Rota about 2,000; both populations are expected to increase rapidly in the next decade with an influx of foreign labor. Aguijan has been uninhabited since World War II. The CNMI is a U.S. commonwealth.

Saipan, Tinian, and Aguijan

The population estimate for Saipan is based on incidental sightings by Division of Fish and Wildlife (DFW) personnel and rare but persistent second-hand reports. The Tinian estimate is from Wiles et al. (1989). The Aguijan estimate is based on two direct counts in August and September 1989 at the only known roost site.

Rota

Direct Counts

We attempted to conduct direct counts at each of four historic colony sites on Rota, quarterly from 1986 through March 1990. We actually conducted 23 direct counts of colonies (2 in 1986, 10 in 1987, 8 in 1988, 2 in 1989, and 1 in 1990). Colony sites were not always occupied, and colonies were not counted when they occupied sites that could not be approached without disturbing the colony. We conducted direct counts when we were able to use an elevated vantage point within 200 m of the colony. We counted bats in colony trees using a 15-60X scope, noting species of tree, location relative to other trees, and the number of bats per tree. We also noted sex and presence of dependant young. In most cases, two of us counted the entire colony, drawing sketches of each tree occupied. If our total counts differed by >5%, we recounted all or a portion of the colony. We added 5%, 10%, 15%, or 20% to the count, depending on distance to colony, amount of foliage, and whether a portion of the colony might be obscured. We believe our population estimates are within 10% of the actual number of bats present.

Departure Counts

We conducted departure counts quarterly (1986-89) at each occupied colony site. This was used to estimate the number of bats in colonies when direct counts were not possible. An observer stationed himself to silhouette the evening flight against the sky. Counts were tallied at 10-min intervals from 1 h before sunset until bats could not be seen with binoculars. Departure totals were multiplied by 2 or 2.5 to get colony estimates because comparisons to direct colony counts at accessible colonies showed this to be a realistic factor. The 2.5 factor was used when two of three variables affecting accuracy (distance to flight path, weather conditions, and visibility, and direc-

tion of flight path relative to the observer) were not optimum.

Extracolonial Counts

We chose 10 extracolonial study sites around the island that ranged in size from 5 to 29 ha. Sites chosen were predominantly native limestone forest, were observable from an elevated vantage point and represented a cross-section of elevation and geographic characteristics. The 10 study plots composed 3.28% of total available bat habitat and 2% of the total land area of Rota. Extracolonial count numbers were extrapolated to get quarterly estimates of the extracolonial population.

Seven of the extracolonial plots were counted monthly and three plots were counted quarterly from December 1987 to November 1988. Counts at all 10 plots were conducted quarterly in 1989. Count periods were from 1600–1730 h, and incidental data were taken after this period. Bats were recorded as entering, leaving, or remaining within the designated areas. Only bats seen leaving or remaining within the area were included in totals because entering individuals might have used another extracolonial plot or been in a colony most of that day.

Population Estimates

We estimated the Rota fruit bat population quarterly by summing the colony estimates (derived from direct or departure counts) and the estimate of the extracolonial population. Data on breeding season, food habits, sex ratios, and social behavior during surveys were also gathered and will be presented elsewhere.

Fruit Bat Imports

Import data were obtained from Division of Quarantine records. These data were categorized by year, place of origin, and size of shipment. The numbers of bats in a few records listing only pounds were estimated using 1.7 bats per pound for Yap (based on the weight of bats confiscated at Saipan; $\bar{x} = 265.9$ g, $n = 122$), 1.88 bats per pound for Palau (G. J. Wiles, Guam Division of Aquatic and Wildlife Resources, personal communication), and 1 bat per pound for the Philippines.

We chose a shipment size of 75 bats to separate shipments intended for resale from those for private consumption (A. I. Palacios, CNMI-DFW, personal communication). Bats in shipments of greater than 75 were considered to be for commercial purposes. Although some smaller shipments were known to be imported for sale, probably portions of larger shipments imported by individuals were intended for private consumption or gifts.

Results

Saipan, Tinian, and Aguijan

Population estimates for the four southern islands are listed in Table 1. Except for Rota, no large roosting or feeding concentrations currently exist, and sporadic poaching incidents continue. A second hand report of young bats in 1989 and the discovery of an injured subadult in 1988 indicate Saipan bats are still managing to reproduce.

A Tinian resident with a farm near a cliffline at Laderan Apaka reported seeing one or two bats occasionally. The largest number reported in recent years is 18, 6 of which were killed by poachers (Wiles et al. 1989). Wiles et al. (1989) estimated that fewer than 25 bats remained on Tinian.

A female with young was sighted on Aguijan in 1989. The number of bats on Aguijan has reached as high as 250–300 in recent years (1988), but this was probably a result of immigration from Rota because of disturbance there (Wiles and Glass 1990). Aguijan, though uninhabited, is subject to poaching.

Rota

Population estimates (Table 2) indicate that the Rota fruit bat population remained fairly stable during the first 20 months of the study, but declined drastically (57%) following disturbances and poaching related to a major typhoon during January 1988. Population estimates during our

Table 1. *Estimated bat populations and area-based carrying capacities of the four islands, 1990.*

Island	Area (km^2)	Estimated carrying capacity[a]	Population estimate
Rota	85.2	4,260	1,067
Saipan	122.9	6,145	<40
Tinian	101.8	5,090	<25
Aguijan	7.2	360	50
Total	317.1	15,855	1,182

[a] Based on a density of 0.5 bats per hectare of seven northern islands (Anatahan, Sarigan, Guguan, Pagan, Agrihan, Asuncion, and Maug; Wiles et al. 1989).

Table 2. *Rota fruit bat population estimates, 1986–90.*

Date	Colony 1	Colony 2	Colony 3	Colony 4	Extra-colonial/ % of total	Total
September 1986	1,365	350	100	10	225 (11%)	2,050
February 1987	361	25	576	576	1,000 (39%)	2,538
April 1987	1,109	60	10	605	427 (19%)	2,211
July 1987	1,720	342	0	65	120 (5%)	2,247
October 1987	1,199	836	150	25	240 (10%)	2,450
January 1988	423	450	42	60	1,620 (62%)	2,595
April 1988	414	178	3	10	457 (43%)	1,062
August 1988	130	360	53	229	305 (28%)	1,077
November 1988	640	460	4	5	318 (22%)	1,427
March 1989	30	170	15	12	640 (74%)	868
June 1989	845	100	2	12	108 (10%)	1,067
September 1989	398	163	0	35	61 (9%)	657
December 1989	323	756	0	41	380 (26%)	1,480
March 1990	590	25	22	45	91 (12%)	773

[a]Colony: 1 = Uzulon Hulo, 2 = As Pupuenge, 3 = Palii, 4 = Sagua Pakpak.

study ranged from a high of 2,595 in January 1988 to a low of 657 in June 1989.

The proportion of fruit bats determined to be outside of colonies during daylight varied during the study. Extracolonial numbers were lower when ripe fruit, particularly breadfruit (*Artocarpus* spp.), was abundant. The percentage of fruit bats living extracolonially varied between 5% (July 1987) and 39% (February 1987) under normal conditions. Immediately following the massive habitat destruction of the typhoon, 62% were living extracolonially.

Fruit bats were observed using 13 species of trees for roosting aggregations. The most commonly used were *Elaeocarpus sphaericus*, *Macaranga thompsonii*, and *Guettarda speciosa* (70% of aggregations counted). Fruit bats on Rota seemed to use any tree species in the roost area. All four currently used colony sites were located at relatively high elevations (320–330 m) and were adjacent to precipitous terrain. Three colonies were immediately adjacent to the sheer walls of the central karst plateau, behind a large limestone rock formation. The fourth was on a gently sloping series of karst ridges which made approach to an overlook impossible.

Imports

Between 1986 and 1989, more than 13,000 bats were imported into the CNMI from eight different points of origin (Table 3). Palau was the source of about half of the bats and was the biggest supplier each year except 1986, when a large number of bats was imported from the Philippines. Most shipments were relatively small (40% ≤ 10 bats; 68% ≤ 25 bats; 87% ≤ 75 bats) and probably were consumed at family gatherings. Bats intended for resale accounted for 56% of bats imported, but only 13% of 334 shipments. Shipments from some points, particularly the Philippines, were usually large and imported by retailers that also sell imported fruits or seafood.

Discussion and Management Implications

Based on area, the southern CNMI islands should be able to support at least 15,000 bats. The high number and diversity of bat food species on Rota suggest that its carrying capacity is higher than our estimate. However, proposed developments may soon transform much of this habitat into resorts and golf courses. The carrying capacity of Tinian may be lower than our estimate because of the greater extent of habitat destruction. Wiles et al. (1989) reported the highest minimum density of 0.95 bats per hectare. Based on a density of 1 bat per hectare, the four southern islands could have supported a minimum of 30,000 fruit bats before the habitat damage by feral animals, agriculture, and development.

Table 3. *Number and origin of Commonwealth of the Northern Mariana Islands fruit bat imports, percent of annual total (in parenthesis), and estimated percent of total commercial imports, 1986–89.*

Date	Palau	Yap	Pohnpei	Chuuk	Kosrae	American Samoa	Western Samoa	Philippines	Total
1986	630 (23.3)	76 (2.8)	46 (1.7)	23 (0.9)	0 (0)	112 (4.1)	423 (15.6)	1,394 (51.6)	2,704 (100)
1987	556 (73.8)	46 (6.1)	35 (4.6)	60 (8.0)	6 (0.8)	50 (6.6)	0 (0)	0 (0)	753 (100)
1988	3,306 (57.9)	1,181 (20.7)	229 (4.0)	79 (1.4)	15 (0.3)	0 (0)	0 (0)	893 (16)	5,705 (100)
1989	2,376 (57.5)	825 (20.0)	677 (16.4)	67 (1.6)	0 (0)	0 (0)	0 (0)	190 (4.6)	4,135 (100)
Total	6,868 (51.7)	2,128 (16.0)	987 (7.4)	229 (1.7)	21 (0.2)	162 (1.2)	423 (3.2)	2,477 (18.6)	13,297 (100)
Commerical Imports	2,771	1,675	468	0	0	0	423	2,177	7,514
Percent of Commerical Imports	40.3%	78.7%	47.4%	0.0%	0.0%	0.0%	100.0%	87.9%	56.5%

Rota

We estimate 60% of Rota (5,080 ha) is forested and constitutes reasonably good fruit bat habitat. Mean fruit bat density during the first 16 months of the study was 0.47 bats per hectare. Because of its more diverse forest, we believe Rota could support a higher density of bats than any of the northern islands. Before the serious decline of 1988, we estimate that Rota's bat population was kept at perhaps 25–50% of its carrying capacity by chronic poaching.

Shifts in location of the largest colonies to inaccessible sites prevented us from conducting direct counts during 1989. These shifts were usually attributed to poaching disturbances. The lower precision of departure and extracolonial counts resulted in estimates that ranged from 657 (September) to 1,480 (December). We suspect the June estimate of 1,067 may be the most accurate estimate. However, poaching has continued and our March 1990 estimate of 773 bats benefited from a direct count at the only known active colony site.

We attribute the precipitous population decline following Typhoon Roy in 1988 to poaching and emigration, rather than storm-related mortality or habitat destruction. We conducted surveys 9–15 days after the typhoon and estimated the population at 2,595. The large number of extracolonial bats during the survey indicated bats were searching for new food sources. After the typhoon, 71 of 83 (86%) bats were observed feeding on *Pandanus fragrans*. The rare use of *Pandanus* before this (one sighting in 12 months) suggests it is a less preferred, emergency food. Bat feeding and activity, other than increased daylight activity, were normal, and bats collected during this period were fat and in prime condition.

The level of poaching following the typhoon was high; we encountered nine poaching parties during 10 field trips. Bats were very vulnerable at this time because trees were stripped of foliage, and bats were more active in daylight. The poaching and disturbance seems to have caused emigration of about 500 bats to other islands. A colony at Guam's Pati Point increased by about 300, and a count on Aguijan during July was 200 above any count of the previous 5 years (Wiles and Glass 1990). Large numbers of bats often shifted between colony sites following known human disturbances of colonies.

An important characteristic in maintaining Rota's current fruit bat population appears to be the presence of extremely precipitous topography available for roost sites. Steep limestone karst formations like those on Rota are largely absent from the other three southern islands in the Marianas.

Imports

Records of fruit bat imports into the CNMI are available beginning with 1986. There were probably imports before this because the Saipan and Tinian bat populations were near extirpation by 1981, but the numbers were probably small. Bats may have been illegally obtained from islands north

of Saipan; however, few boats were capable of reaching there until recently (Palacios, personal communication). The import trend for the next few years may be upward with the increase in disposable income from recent rapid development. However, eating bats may be losing its appeal to young people; some consider it a custom of old people.

The decrease in imports in 1987 cannot be entirely explained. However, one retailer who imported almost 1,400 bats from the Philippines in 1986 found Philippine bats unpopular with consumers and he stopped importing them (Palacios, personal communication). Also, no bats were imported from Western Samoa in 1987. These sources account for most of the decrease in imports in 1987. Price increases and changes in suppliers or quarantine personnel may account for the rest of the difference. Imports significantly increased in 1988, perhaps because many residents obtained instant wealth by selling land to developers.

Palau was the source of about half the imports where bats receive no legal protection, and many CNMI residents have family ties. Yap was the source of 2,128 bats although a hunting moratorium has been in effect since 1981 (except a one month season on Ulithi in 1988; M. Falanruw, U.S. Forest Service, personal communication). CNMI Division of Quarantine inspectors began requiring export permits or certificates of origin for bat imports in mid 1989 at the request of the Division of Fish and Wildlife. Undocumented shipments are now detained and confiscated by conservation officers.

The change in status of seven *Pteropus* species in 1989 from Convention on International Trade in Endangered Species (CITES), Appendix II to Appendix I will change points of origin and perhaps numbers of bats imported. Commercial shipments of Appendix II bat species from New Guinea, the Solomons and the Philippines may supply the market in the future, replacing those from the Federated States of Micronesia. If these changes increase the price of bats significantly, poaching pressure, particularly on Rota and the northern Mariana Islands may increase and require sharply increased enforcement efforts.

Recommendations

Education efforts in all aspects of conservation, but particularly concerning island bat populations, need to continue and be increased. Wildlife law enforcement efforts need improvements, and a precedent of convictions must be established. Trained and effective conservation officers hired and controlled by the Division of Fish and Wildlife, not local politicians, need to be stationed on the inhabited islands. Effective procedures for enforcing regulations on the uninhabited CNMI islands need to be developed and implemented. Local regulation of legal bat imports, including shipment size and quota restrictions, must be implemented to avoid overexploitation of source populations.

The fruit bat populations of the southern CNMI face several serious threats. Poaching continues to be a serious problem on Rota and may increase on remote islands as imports are restricted. The brown tree snake (*Boiga irregularis*) is a predator of fruit bats on Guam (G. J. Wiles, personal communication) and may reach the CNMI in cargo and become established. Habitat reduction by development is a certainty. These combined threats lead us to believe bat populations on the southern islands of the CNMI warrant listing on the Federal Endangered Species List. However, this would only be effective if federal enforcement assistance resulted.

Research needs include determining seasonal habitat requirements and sustainable harvest of *Pteropus mariannus*. Areas of limestone forest and cliffline roosting sites need to be protected from development if these islands are to have significant populations of fruit bats in the future.

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Status of the Marianas Fruit Bat (*Pteropus mariannus*) in the Northern Mariana Islands North of Saipan

by

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Abstract. Populations of Marianas fruit bats, *Pteropus mariannus*, were systematically surveyed for the first time on 10 remote islands north of Saipan in 1983–84. More recent information is used to update the original population estimates when available. A minimum total population estimate of 7,450 fruit bats is derived using evening dispersal counts (EDC's), bat flyway counts (BFC's), and bat roost counts (BRC's). Population size was compared with island size and the level of hunting intensity for southern versus northern islands. Bat populations appeared at much higher densities on lightly hunted islands. Fruit bat populations for heavily and lightly hunted islands increased in similar proportions with increasing island size. In addition to illegal hunting, other threats to bat populations include volcanic activity, typhoons, military training, human development, introduced predators, and feral herbivores. Illegal hunting remains the greatest threat to fruit bats and possibly one of the few factors that can be controlled by human intervention. Repeatable systematic surveys of northern island fruit bat populations every 3 years is one of four recommendations.

Two species of mammals are native to the Northern Mariana Islands, the Marianas fruit bat (*Pteropus mariannus*) and a small insectivorous sac-winged bat (*Emballonura semicaudata*). Both species have experienced dramatic declines in numbers and face threats to their survival (Ralph and Sakai 1979; Lemke 1986a, 1986b). Two subspecies of *P. mariannus* have been described from the Commonwealth of the Northern Marianas Islands, *P. m. mariannus* from Rota, Aguijan, Tinian, and Saipan (Kuroda 1940), and *P. m. paganensis* from Pagan and Alamagan (Yamashina 1932). The taxonomic status of *P. mariannus* populations on other islands north of Saipan has not been determined.

The decline of fruit bats in the U.S. Commonwealth of the Northern Mariana Islands (CNMI) and on neighboring Guam has been largely attributed to overharvesting of bats for food (Perez 1972; Wheeler and Aguon 1978; Ralph and Sakai 1979; Wheeler 1979, 1980; Wiles 1987a). Fruit bats are an important food item in the local Chamorro culture. Demand for fruit bats led to a commercial trade in dead bats that affected fruit bat populations not only in the Marianas but also in several other island groups in the Pacific (Wiles and Payne 1986).

The CNMI fruit bats have been protected by local laws since 1977. It has been illegal to harvest bats except for a few specially permitted hunts on Rota and Anatahan. In 1988, the U.S. Fish and Wildlife Service determined that endangered species status for *P. mariannus* populations on Saipan, Tinian, and Aguijan was warranted but precluded by other listing priorities (U.S. Fish and Wildlife Service 1988). Presumably, federal protection of these populations will occur in the near future.

The purpose of my study was to census *P. mariannus* on the Northern Mariana Islands north of Saipan, where there have been no previous surveys of fruit bats. Before this effort, concern existed that

hunting had already depleted the bat populations on these remote islands. Examination of fruit bat habitat and populations allowed me to identify other potential and present threats to fruit bats north of Saipan.

Study Area

The Northern Mariana Islands lie between 13° and 21° N and between 144° and 146° E in the western Pacific Ocean (Fig. 1). Politically, the 14 islands fall within the U.S. Commonwealth of the Northern Mariana Islands. The islands are volcanic in origin with limestone deposits on southern islands. Maximum elevations of the islands vary from 81 m on Farallon de Medinilla to 965 m on Agrihan, the highest island in Micronesia. The vegetation, geology, and topography are described elsewhere (Fosberg 1960; Eldredge 1983).

The northern islands are characterized by rugged terrain with steep slopes and ravines, thick forest or shrub vegetation, and large areas of swordgrass, *Miscanthus floridus*. Native vegetation has been altered at many sites by planting of coconut (*Cocos nucifera*) groves; by introduction of exotic fruit trees, ornamental flowers, and weeds; and by the release of goats, pigs, and cattle, which have established feral populations. Since the early 1800's volcanic activity transpired on 6 of the 10 islands north of Saipan (Eldredge 1983). Permanent human populations reside only on Agrihan, Alamagan, and Anatahan, with frequent human visitation to Pagan. The total population is usually less than 75 people.

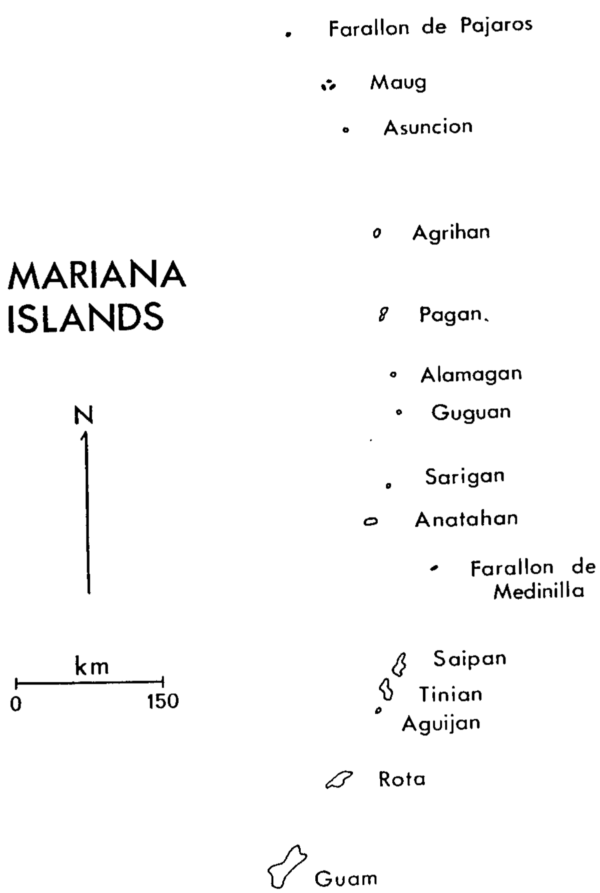

Fig. 1. Map of the Mariana Islands in the western Pacific Ocean.

Methods

A survey team of six people visited all the islands north of Saipan except Maug and Farallon de Medinilla by boat from 17 August to 10 September 1983 (Anonymous 1984). Maug and Farallon de Medinilla were surveyed from 19 February to 5 March 1984. Many of the other islands were revisited during the 1984 trip, and since then, to gather additional data on fruit bats (Wiles et al. 1989).

Data from the Mariana Islands south of Farallon de Medinilla indicated that a large proportion of fruit bats typically roost gregariously in treetop colonies during the day. Emphasis during northern island surveys was placed on locating major fruit bat colonies on each island and counting the number of bats in each roost. On some islands bats did not live in large colonies but rather in much smaller scattered groups or as roosting individuals.

Bats were counted with three methods. Bat roost counts (BRC's) were direct counts of bats as they hung in roost trees during the day. This technique was of limited use because of thick vegetation and the distances involved in observing bats in rugged terrain. Evening dispersal counts (EDC's) attempted to tally bats as they dispersed from colonial roost sites in the late afternoon and evening. EDC's were the most frequently used and perhaps the most accurate method when colonies could be located and dispersal occurred before total darkness. Bat flyway counts (BFC's) were a modification of dispersal counts. When large colonies did not exist, observers positioned themselves in good locations to watch for individual bats as they soared over the forest canopy or along major ridgelines in their search for food. In many cases experience was gained from one night to the next that led to improved counts. Occasionally, local resi-

dents were interviewed for information on where bats roosted. A discussion of field survey techniques is presented elsewhere (Wiles et al. 1989).

Population estimates of fruit bats for individual islands were based on several factors, including number of bats counted, size of the island, amount of forest cover, and food plant diversity and abundance. On larger islands where EDC's were the main censusing method, population estimates of fruit bats were often higher than the actual counts. The rationale for this was that EDC's at colonies would not account for all the bats in the colony or the bats not associated with the colonies. On islands where no colonies were found and all counts were of foraging bats, population estimates tended to be similar or lower than the number of bats recorded. Whenever possible, duplicate sightings were factored out of the counts and estimates.

Table. *Minimum population estimates of* P. *mariannus for islands north of Saipan, 1983–84.*

Island	Area (km^2)	Number of bats counted	Minimum population estimate	Minimum population density (bats/ha)
Farallon de Medinilla	0.9	0	0	0.0
Anatahan	32.3	1,204	3,000	92.8
Sarigan	5.0	213	125	25.0
Guguan	4.2	150	400	95.2
Alamagan	11.3	0	0	0.0
Pagan	48.3	1,339	2,500	51.8
Agrihan	47.4	517	1,000	21.1
Asuncion	7.3	394	400	54.8
Maug	2.1	0	25	11.9
Farallon de Pajaros	2.0	0	0	0.0
Total	160.8	3,817	7,450	—

Results

Population Estimates

General comparisons and estimates are summarized in this section. Detailed island by island results are available in Wiles et al. (1989). Fruit bats inhabited seven islands north of Saipan (Anatahan, Sarigan, Guguan, Alamagan, Pagan, Agrihan, and Asuncion), were suspected to appear in small numbers on one island (Maug), and were absent from two islands (Farallon de Medinilla and Farallon de Pajaros; Table).

During the original 1983–84 surveys no fruit bats were located on Alamagan. At the time, local residents believed the bats migrated to nearby Pagan. In March 1988, Division of Fish and Wildlife personnel from Saipan reported moderate numbers of bats, but no attempt was made to estimate numbers. The small island of Maug (actually three adjacent islets) has been known to harbor a small number of fruit bats in recent years (Eldredge et al. 1977). In 1981, the island was hit by a typhoon that destroyed much of the forest vegetation. I did not discover bats on Maug, however, I believe the islets probably support a small population of fewer than 25 bats in the remaining habitat.

Three islands (Anatahan, Pagan, and Agrihan) support large bat populations estimated to be at least 1,000–3,000 bats each (Table). Several major bat colonies were located on these islands, which have provided large numbers of fruit bats for the commercial trade. Guguan and Asuncion had moderate numbers of bats, while Sarigan supported about 125 fruit bats.

Farallon de Medinilla, although lacking good forest habitat, had small numbers of fruit bats before the mid-1970's, when the U.S. Navy began bombing and artillery practice on the island. Habitat destruction has been extensive, and fruit bats are no longer present. The northernmost island, Farallon de Pajaros, is an active volcano covered almost entirely by barren volcanic debris. There is no suitable bat habitat on this island.

In terms of minimum population density, Anatahan, Guguan, and Asuncion ranked highest with 93, 95, and 55 bats per hectare. Guguan and Asuncion are relatively small islands (<10 km^2) with excellent habitat capable of supporting relatively high numbers of bats. Anatahan is a large island (32 km^2) with good forest habitat that supports the largest single bat population of at least 3,000 bats.

Population Densities of Fruit Bats Among Islands

Population sizes and densities of fruit bats were compared among islands according to hunting intensity. The southern islands of Guam, Rota, Aguijan, Tinian, and Saipan have experienced heavy islandwide hunting pressure because of large resident human populations or proximity to population centers. Fruit bat populations on these islands were

compared to islands north of Saipan. Data from four northern islands were excluded because of volcanic activity (Farallon de Pajaros), military bombing activity (Farallon de Medinilla), or recent typhoon damage (Maug), or because the bat population was too poorly known for inferences to be made (Alamagan).

Population sizes were linearly related to island size for islands north of Farallon de Medinilla ($r = 0.733$, $P = 0.03$), where hunting happens irregularly, but were slightly more variable among the heavily hunted southern islands ($r = 0.513$, $P = 0.17$; Fig. 2). Comparisons of the two regressions revealed a difference in the y-intercept ($F = 24.3$, $P = 0.005$), but no difference existed in the slopes of the lines ($F = 0.025$, $P = 0.75$). These data indicate that bat populations are at much higher densities on lightly hunted islands, but that populations for the two groups of islands increased in similar proportions with increasing island size. Estimated densities of bats were highest on the northern islands, ranging from 21.1 to 95.2 bats per hectare. In contrast, densities were much lower on

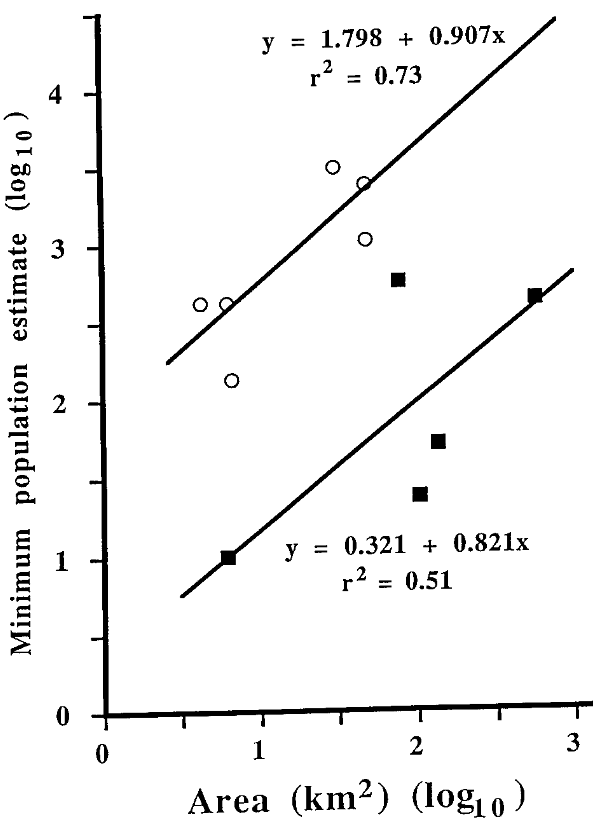

Fig. 2. Relations between the sizes of heavily hunted (*closed squares*) and lightly hunted (*open circle*) populations of Marianas fruit bats and island size in the Mariana Islands.

the southern islands, varying from 0.2 to 11.7 bats per hectare (Table).

Present and Potential Threats to Fruit Bat Populations and Habitat

In addition to illegal hunting mentioned above, fruit bats and their habitats in the northern islands are potentially threatened by other natural and human-related factors.

Volcanic activity on Farallon de Pajaros and Asuncion in the early 1900's and on Pagan in 1981 destroyed areas of suitable fruit bat habitat and, presumably, may have caused direct mortality or losses because of emigration. Habitat alteration because of lava and ash-fall has long-term effects. Major soil-building and plant succession must take place before volcanic areas are used again by bats.

Periodic typhoons devastate native forests bats depend on for food and roost sites. Typhoons that hit Maug in 1981 and Rota in 1988 had severe effects on bat habitat. Fruit bats are particularly vulnerable to hunting following typhoons. Bats will forage desperately throughout the day, often landing on or near the ground without the typical avoidance of humans. Depending on the time of year, important food sources may be lost. Typhoons may be a factor in interisland movements and colonization of new habitats.

United States military training activities on Farallon de Medinilla have removed a certain amount of fruit bat habitat from the archipelago. Increasing military presence and use of the CNMI for training may, in the future, jeopardize fruit bat and other wildlife habitat.

Introduced predators and feral herbivores may alter natural communities in ways that are deleterious to fruit bats. The brown tree snake (*Boiga irregularis*), an introduced species now well established on Guam, has decimated native avifauna and has been implicated as a possible predator on juvenile fruit bats (Wiles 1987b). The brown tree snake apparently arrived on Guam by cargo ships from New Guinea or the Soloman Islands in the 1940's or early 1950's (Savage 1988). Introduction of this species into the CNMI by shipments from Guam or elsewhere is a distinct possibility and a concern expressed by the CNMI Division of Fish and Wildlife (Federal Pittman-Robertson job progress report 1987).

Six of the 10 northern islands have populations of feral goats or pigs. Pagan also has a small number of feral cattle. These animals are the result of intentional or accidental releases that may date back to Spanish explorers or, more probably, German and Japanese occupation of all remote islands between 1898–1944. Feral livestock, particularly goats, had a negative effect on the regeneration of native forest vegetation, including important fruit-producing species bats depend on. On islands such as Sarigan, where goats are abundant, the native forest shows little sign of effective regeneration. Changes in native flora may have subtle but long-term negative effects on bats as well as other species.

The harvesting of bats for food continues to be the most serious threat to fruit bats on the more remote islands north of Saipan. In the late 1960's and through the 1970's, untold thousands of bats were harvested in the northern islands. Entrepreneurs from Guam provided northern island residents with guns, ammunition, and financial incentives to harvest as many bats as possible (D. Aldan, personal communication). From 1975 to 1981 (excluding 1977) import records indicate 15,805 fruit bats were shipped into Guam from the CNMI (Wiles and Payne 1986). Most shipments were listed as coming from Saipan and Tinian; however, by 1975 those populations were already very low. Many of the bats were probably killed in the northern islands and transhipped through Saipan and Tinian. Beginning in 1982 it became illegal to ship bats from the CNMI to Guam because of local legislation that listed Guam's population of *P. mariannus* as endangered. Subsequent shipments of bats from the CNMI were shipped secretly or given false points of origin.

Recommendations

Over 80% of the fruit bats in the entire Mariana archipelago (including Guam) inhabit the remote islands north of Saipan (Wiles et al. 1989). On all of the other islands, fruit bats have experienced significant population declines and are, to varying degrees, in danger of extinction. The following management recommendations are made to protect existing fruit bat populations north of Saipan, which may ultimately provide a source of bats for recovery elsewhere in the Mariana Islands:

1. Resurvey fruit bat populations on all northern islands every 3 years, begin immediately. Develop a repeatable procedure for each island, using effective vantage points and known colony and flyway locations. Experiment with more effective survey techniques as they are developed. Use population trend data to evaluate present species status. If warranted, use survey information to recommend additional protection (federal listing or sanctuary areas) or to establish limited entry fruit bat hunts.
2. Increase efforts to educate the public regarding the conservation of their natural resources. The program should emphasize what has happened to fruit bats in the CNMI with unregulated hunting, the importance of bats to island ecosystems, and the cultural significance of the species.
3. Conduct trial hunting seasons when feasible, under strict quotas and regulations, on islands that can support a limited harvest of bats (possibly Anatahan, Pagan, and Agrihan). There should be a positive incentive to fruit bat conservation. People need to understand that there are tangible rewards and benefits associated with wildlife management.
4. Bolster the local enforcement program by hiring additional people and providing adequate training for all conservation officers. Increase inspection efforts for all vessels and aircraft visiting the northern islands.

Acknowledgments

The initial 1983 survey trip was largely financed by the Oxford University Expedition to the Mariana Islands. This expedition received funds and equipment from the Oxford University Chest and Department of Zoology, the Alexander Allan Paton Fund, the Biological Council, the British Ecological Society, the Ely Webster Trust, the Fauna and Flora Preservation Society, the Gilchrist Education Fund, Konishuroku (U.K.) Ltd., the Marian Hewitt Fund, the Queen's College (Oxford), the Radleian Society, S. R. Gent, the World Wildlife Fund, and a number of smaller donors. Additional funding for the 1983 survey and subsequent surveys was provided by the U.S. Fish and Wildlife Service Federal Aid to Wildlife Restoration Program, Project W-1-R-2 for the CNMI and Project FW-2R-20 for Guam.

D. T. Aldan, L. M. Adam, D. Batty, N. H. Payne, T. K. Pratt, and G. J. Wiles assisted in collecting data in 1983 under difficult field conditions. Subsequent field data were collected by D. T. Aldan, C. Falig, P. O. Glass, and T. K. Pratt.

R. Lujan and A. I. Palacios, when each was in his position as Chief of the CNMI Division of Fish and Wildlife, supported fruit bat research and protection in a difficult political environment. Their efforts have been and continue to be of critical importance.

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The Flying Foxes *Pteropus samoensis* and *Pteropus tonganus*: Status in Fiji and Samoa

by

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Introduction

Fiji and Samoa are known for two species of fruit bats, or flying foxes (Andersen 1912). Traditionally, these two species (*Pteropus tonganus* and *P. samoensis*) have been hunted for food on these islands. Recently, bats have been harvested commercially and shipped to Guam from Samoa and many other islands (Wiles and Payne 1986). This added take from market hunting, coupled with a continuing loss of native forest habitat, caused concern that the less common of the two species, *P. samoensis*, might be endangered (Cox 1983).

In November 1984, a petition was submitted to the U.S. Fish and Wildlife Service (USFWS) to add *P. samoensis* to the U.S. Endangered Species List. In June and July 1985, USFWS personnel conducted limited field studies in American Samoa and gathered data suggesting that *P. samoensis* was more common than indicated in the petition. As a result, a finding of "warranted but precluded" was designated for the Samoan population of this bat.

From 19 June to 7 August 1986, additional field data were gathered by a team of four USFWS biologists. Assistance was provided by the American Samoa Office of Marine and Wildlife Resources and the Western Samoa Division of Forestry. The survey team spent 25 days on Tutuila, 8 on Ta'u, 8 on 'Upolu, 5 on Ofu and Olosega combined, 2 on Savai'i, and 1 on Aunu'u (Figs. 1–4). Based partly on the results of this survey, the population was classified as a candidate endangered species by the USFWS in 1988.

From 16 July to 15 August 1989, we surveyed both species in Fiji and Samoa. Using identical methods to obtain comparable data, we resurveyed 50 sites in Western and American Samoa that had been examined in 1986. We summarize all survey results herein.

The taxonomy and ecology of the two species of *Pteropus* in Fiji and Samoa have been unclear. *Pteropus tonganus* was described from Tonga (Quoy and Gaimard 1830). It was first reported from Fiji (as *P. keraudrenii*) by Schmeltz (1864) and from Samoa (as *P. flavicollis*) by Alston (1874). *Pteropus samoensis* was described from Samoa by Peale (1848), who first reported it from Fiji (as *P. keraudrenius*) as well (Peale 1848).

Although two species have been known to occur on both Fiji and Samoa for more than 100 years (Gray 1870; Alston 1874), many naturalists have assumed that there was only a single species

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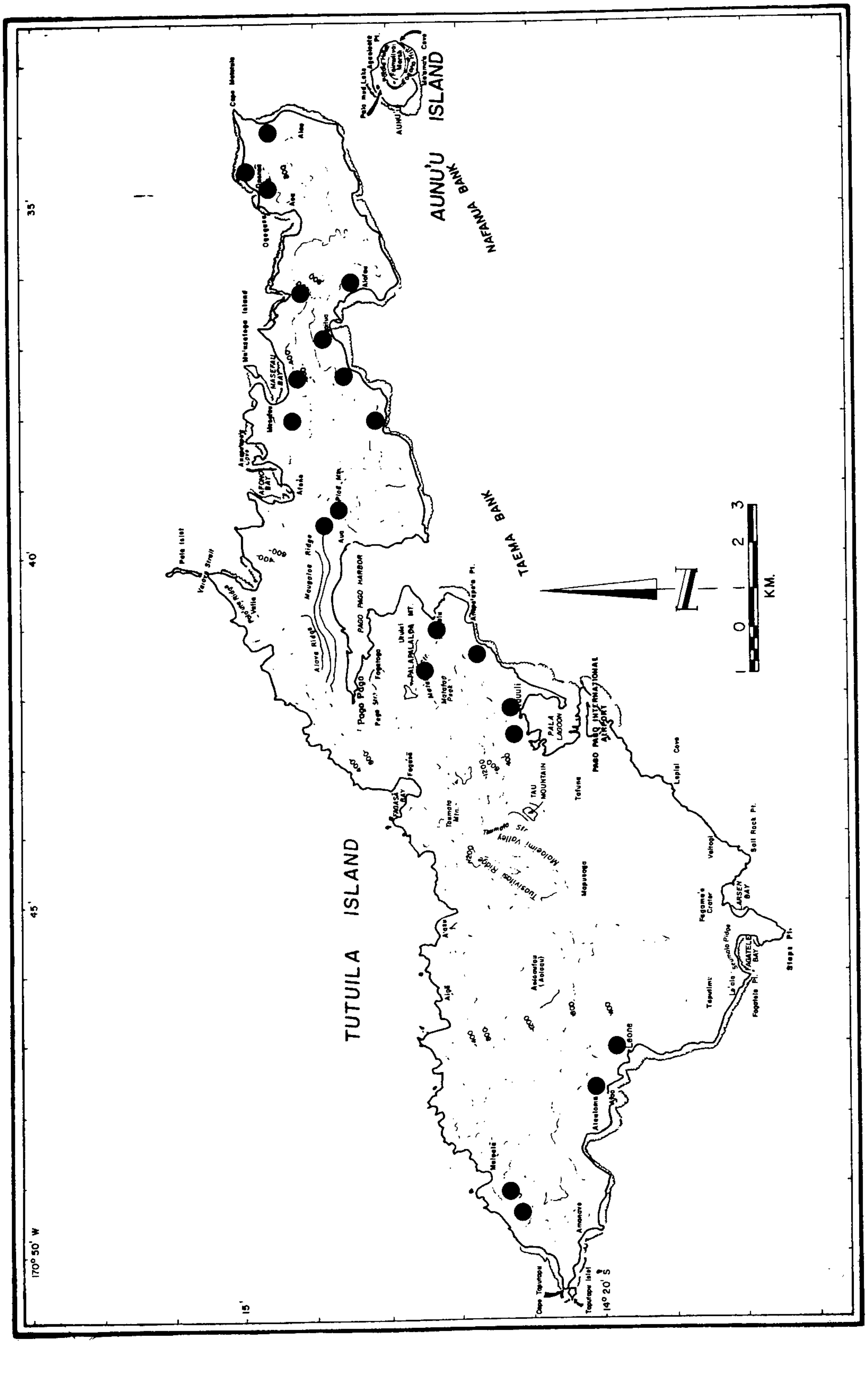

Fig. 1. Tutuila Island, American Samoa, showing the 21 stations surveyed for fruit bats.

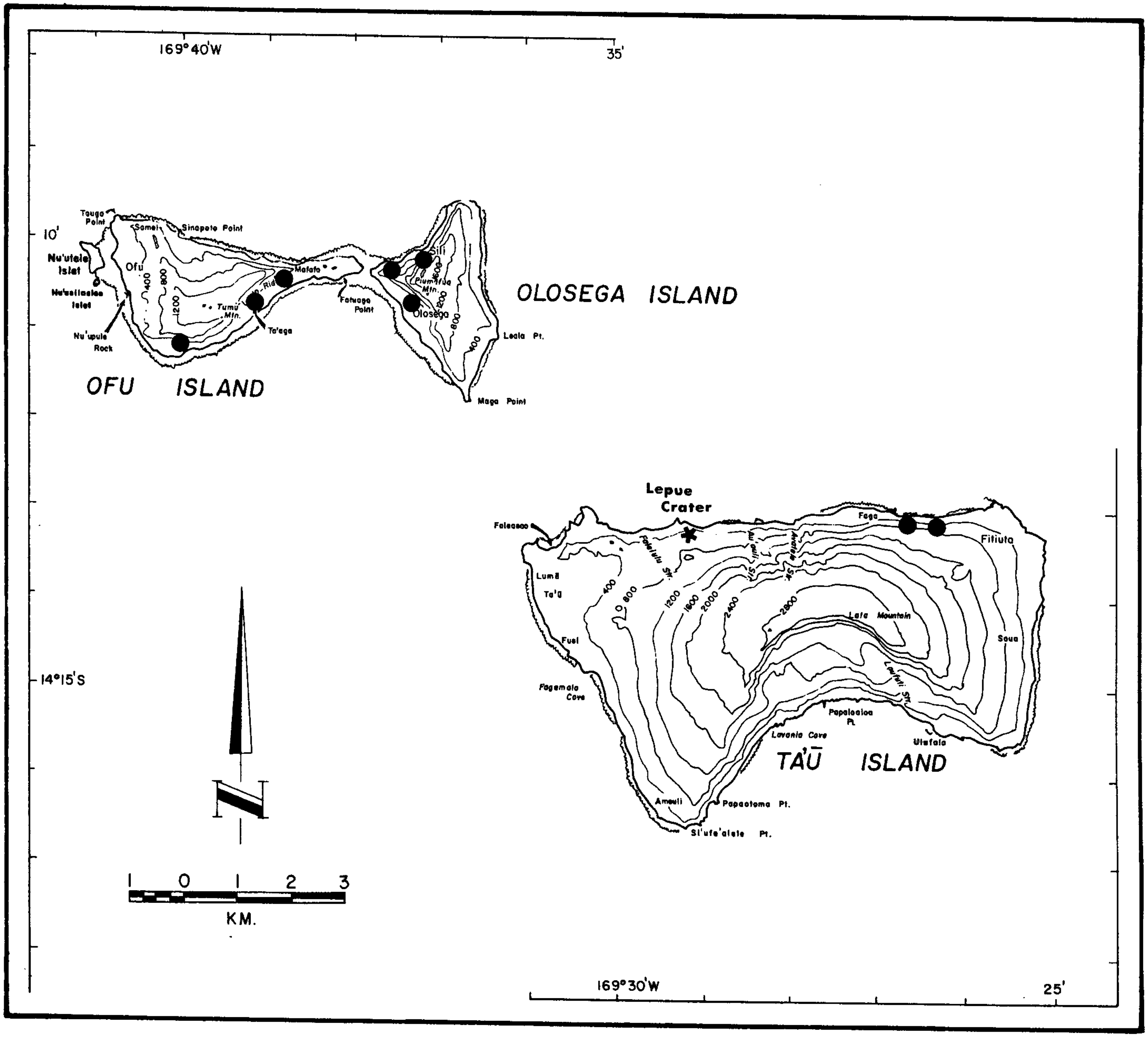

Fig. 2. The Manu'a Islands (Ofu, Olosega, and Ta'u), American Samoa, showing the eight stations surveyed for fruit bats. Lepue Crater site was counted only

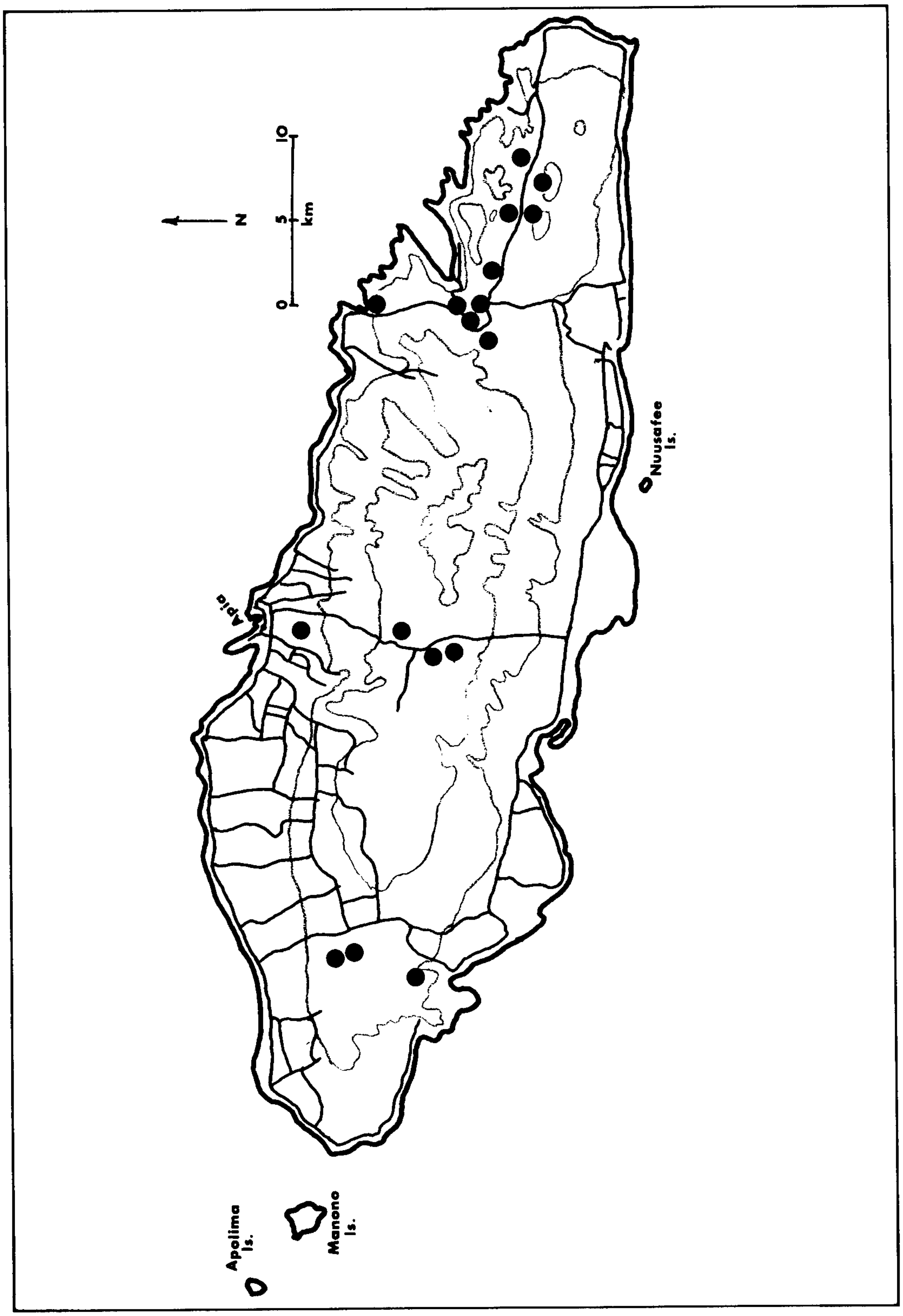

Fig. 3. 'Upolu Island, Western Samoa, showing the 17 stations surveyed for fruit bats.

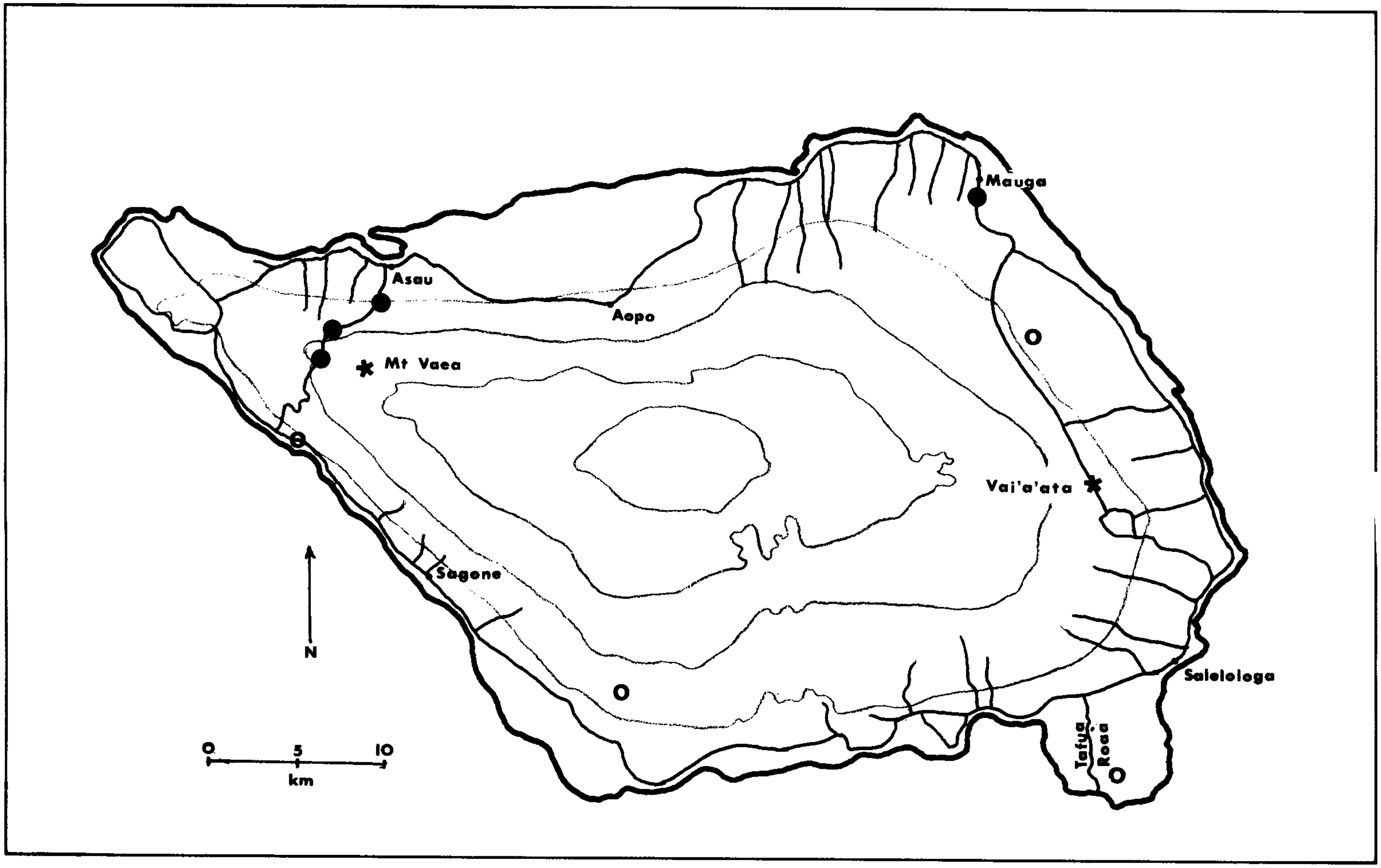

Fig. 4. Savai'i Island, Western Samoa, showing the six stations surveyed for fruit bats. All-day counts (*) were conducted at Mt. Vaea and Vai'a'ata in 1989.

present. Several additional names have been proposed for *Pteropus* from Fiji and Samoa, but all are now considered synonyms of either *P. tonganus* or *P. samoensis*.

Ecological observations have frequently been attributed to the wrong species. Whitmee (1875) reported a group of more than 1,000 individuals on Savai'i as *P. whitmeei* (= *P. samoensis*), but they were almost surely *P. tonganus*. Similarly, Nicoll (1908) was probably observing both species on Tutuila but reported all as *P. ruficollis* (= *P. samoensis*).

This taxonomic confusion continued. Amerson et al. (1982) reported a population estimate of 140,700 for *P. samoensis* on American Samoa. This figure seems inflated, even allowing for the inclusion of all observations of *P. tonganus*. The seriousness of this type of misinformation is understood only when subsequent estimates of correctly identified *P. samoensis* reveal a fraction of that number. The magnitude of the apparent decline in numbers is far out of proportion to reality, and probably masks a smaller-scale, but still serious, decline in the population of *P. samoensis* in recent years.

Cox (1983) presented the first detailed ecological observations correctly attributable to *P. samoensis*. Although he identified several differences between the two species, his speculations on body size, habitat use, population size, and primary activity period were perhaps prematurely conceived.

Characteristics that allow correct field identification of the two species have yet to be detailed. Consequently, our first goal was to determine and describe such field traits. Then, with a clear impression of how to identify the two species, we concentrated on determining the status of *P. samoensis*, the less common of the two species. Nevertheless, we also recorded observations of *P. tonganus* on Fiji and Samoa.

Description of Study Sites

The Samoan Islands, located in the South Pacific (14° S, 170° W), are a biogeographical unit politically divided into American Samoa, an unincorporated territory of the United States, and Western Samoa, an independent country. About 35,000 people live in American Samoa, where the economy is based largely on government jobs, tuna canneries, and tourism (Anonymous 1987). American Samoa comprises four major islands: Tutuila (Fig. 1), Ofu, Olosega, and Ta'u. Ofu, Olosega, and Ta'u are collectively known as the Manu'a Islands (Fig. 2). Land area is about 195 km^2, 75% of which is on the main island of Tutuila (Anonymous 1987). The islands are steep and rugged. The highest point is on Ta'u (966 m). The capital, Pago Pago, is located on Tutuila.

Western Samoa is composed of two main islands: 'Upolu (1,115 km^2) and Savai'i (1,814 km^2). Their combined area, 2,929 km^2, is nearly 15 times the land area of American Samoa. 'Upolu (Fig. 3) and Savai'i (Fig. 4) have extensive coastal plains, which have been converted to agriculture in most areas. The maximum elevation is 1,860 m on Savai'i. Savai'i is still volcanically active, and a number of recent lava flows are found there. The capital city, Apia, is on 'Upolu. About 90% of the 163,000 people in Western Samoa are involved in agriculture, major exports being copra, cocoa, bananas, and timber (Adams 1985b).

Fiji comprises a group of 322 volcanic islands lying about 1,000 km southwest of Samoa and 1,770 km north of New Zealand. The islands range in size from Viti Levu (10,388 km^2), on which the capital, Suva, is located, to mere rocks a few square meters in area. Barely more than 100 of the islands are inhabited. The larger islands are mountainous, some rising abruptly from the shore to heights of 1,200 m or more. On the windward (southeastern) side, where rainfall is heavy (up to 305 cm annually), the islands are covered with dense, tropical forests that are rapidly disappearing. Leeward lowlands, which have less timber, are sheltered by the mountains and have a well-marked dry season favorable to crops such as sugar. More than half the population of about 700,000 lives on the island coasts, and about half the work force is involved in agriculture, the major exports being sugar, copra, and gold (Adams 1985a).

Climate

Samoa is in the tropics and is warm and humid. There is considerable variation in climate depending on elevation and exposure to trade winds. The average annual temperature ranges from 21° to 27° C, the warmer temperatures occurring at the lower elevations. Rainfall ranges from 200 cm at the lower elevations to 750 cm at the usually cloud-shrouded upper elevations. Trade winds prevailing from the east and southeast blow most of the year; the monthly average wind speed is 7–18 kph (Amerson et al. 1982).

Fiji is also tropical; it is warm and humid on the windward side, warm and dry on the leeward. On the larger islands of Viti Levu and Vanua Levu, the climate varies dramatically from one side to the other. The average annual temperature is 25° C, with little seasonal change. Rainfall ranges from 100 cm annually in western Fiji to about 300 cm in Suva. Average annual rainfall exceeds 500 cm in many parts of the interior southeastern slopes of Viti Levu and Vanua Levu, and on the corresponding slopes of Taveuni it may exceed 750 cm. The trade winds are mainly southeasterly (Smith 1979).

Vegetation

The natural vegetation of American Samoa consists of tropical rain forest, which is characterized by tall, broadleaf evergreen trees, abundant woody vines, and ubiquitous epiphytes (Amerson et al. 1982). Within this broad classification are a number of plant communities that reflect differences in slope, elevation, microclimate, soil type, and exposure to salt water. Amerson et al. (1982) described 13 different plant communities in American Samoa. The most extensive of these include cultivated land (40%), rain and ridge forest (26%), and secondary forest (20%). Rain forest is defined as the natural vegetation of Samoa. Ridge forest is defined as the forest growing on ridges; it supports many of the same plant species as rain forest but is less well developed because of the higher degree of slope. Secondary forest includes all those stages of forest that have become established after agricultural land has been abandoned. If undisturbed long enough, it will revert to a forest that is virtually indistinguishable from the native rain forest. Cultivated land consists primarily of plantation land, which is mainly diverse agricultural forest. These agricultural forests consist largely of coconuts, bananas, breadfruit, taro, and other vegetation commonly associated with subsistence agriculture. They are often partly overgrown by secondary forest.

Most of the vegetation types described for American Samoa are also found in Western Samoa. There are no detailed vegetation maps currently available for Western Samoa. Most of the steep peaks near the interior support native forests. In 1982, 38% of 'Upolu and 59% of Savai'i consisted of rain forest (M. Iakopo, Western Samoa Forest Service, unpublished report). It is our subjective impression that comparable figures are much lower today, particularly for 'Upolu. Much of the remainder of the land consists of agricultural forest. On 'Upolu, most of the coastal lowlands up to an elevation of 300–500 m have been converted to cultivated land. Savai'i is less heavily populated, and more of that island remains naturally forested.

The vegetation of the large islands of Fiji is strikingly different in the windward and leeward areas. Four very generalized types of vegetation can be discerned. Beach vegetation is similar to that found throughout the tropical Pacific. Large tracts of mangrove forest occur near the mouths of the larger rivers and along muddy coasts. Dry zone vegetation occurs on the leeward coasts of the large islands and inland up to an elevation of about 500 m. Eroded slopes covered with grasses, ferns, shrubs, and scattered small trees are probably the result of repeated burning of the original light forest or shrubby growth. Valleys and ravines contain many trees, possibly similar to the original cover of much of the dry zone. The main dividing range of Viti Levu lies east of the Singatoka Valley, roughly separating the wet and dry zones. Intermediate zone vegetation occurs in broken areas just leeward of the higher forested regions of the large islands. The leeward slopes are covered with grasses and shrubs, while the windward slopes maintain a light, comparatively open, forest. Wet zone vegetation, primarily rain forest, is found on the windward sides of the larger islands. More than half the land area of Fiji is forested (Smith 1979).

Survey Methodology

To establish an index on which to base population trends of *Pteropus samoensis*, we conducted daytime counts from stations with a commanding view of representative native or agricultural forest. At each station a 30-min count was made by one or more observers. Data recorded included the time of each observation and the estimated distance to each bat seen. Counts were conducted throughout the daylight.

We also counted individuals of *P. tonganus* observed during these surveys, but we normally saw them only early in the morning or late in the afternoon. We made some attempt to locate roosts of *P. tonganus* and to count the number of individuals in those roosts. Incidental information was gathered on field identification, feeding behavior, habitat use, and other ecological variables. Data

on hunting was gathered primarily by questioning local residents.

Results and Discussion

Taxonomy and Distribution

Pteropus samoensis Peale, 1848.

Pteropus keraudrenius Peale, 1848. Misidentification (not *Pteropus keraudren* Quoy and Gaimard, 1824).

Pteropus samoensis Peale, 1848. Type locality Tutuila, American Samoa.

Pteropus nawaiensis Gray, 1870. Type locality Nauai, Fiji Islands.

Pteropus vitiensis Gray, 1870. Type locality Ovalau, Fiji Islands.

Pteropus whitmeei Alston, 1874. Type locality Samoa.

Pteropus ruficollis Nicoll, 1908. Part, *nomen nudum.*

Pteropus rufficollis Nicoll, 1908. Part, *nomen nudum.*

Pteropus samoensis was described by T. R. Peale (1848). Peale served as a naturalist on the United States Exploring Expedition under the command of Captain Charles Wilkes. He obtained numerous specimens, several of which are still extant in the National Museum of Natural History. Peale also obtained at least one specimen of *P. samoensis* from Fiji. That specimen still exists in the national collection. Peale identified the specimen as *Pteropus keraudrenius*, a name now in the synonymy of *Pteropus mariannus*. At some unknown later time, a label identifying the specimen as *P. mariannus* was affixed to the specimen, probably as a result of the name *P. keraudrenius* being placed in the synonymy of *P. mariannus*. The specimen has been maintained in the collection with *P. mariannus* ever since. Andersen (1912) mistakenly associated Peale's record with *P. tonganus*, the most common species known from Fiji at that time. Gray (1870) described *P. nawaiensis* and *P. vitiensis* from Fiji in his catalogue of the collections in the British Museum. Both of Gray's names are synonyms of the earlier named *P. samoensis*, although *nawaiensis* is currently recognized as the valid Fiji subspecies, *P. samoensis nawaiensis*.

Pteropus whitmeei, described by Alston (1874), is also a junior synonym of *P. samoensis*. Nicoll (1908) used the name *P. ruficollis* without providing a diagnosis or description, thus rendering it a *nomen nudum*. In the index of that work, he used the spelling *P. rufficollis*, also a *nomen nudum*. As an added complication, his observations make it clear that he had seen both species (*P. samoensis* and *P. tonganus*) and assumed them to be the same.

Currently, the accepted name for the Samoan population is *Pteropus samoensis samoensis*, and for the Fijian population, *Pteropus samoensis nawaiensis* (Wodzicki and Felten 1975).

Pteropus samoensis samoensis is known from all the major islands in both American and Western Samoa. We found them on Tutuila, Ofu, Olosega, Ta'u, Savai'i, and 'Upolu. *Pteropus samoensis nawaiensis* is known from several islands in Fiji—Viti Levu, Vanua Levu, Ovalau, Nauai—and probably occurs on many more. We surveyed only on the largest island, Viti Levu.

Pteropus tonganus Quoy and Gaimard, 1830.

Pteropus tonganus Quoy and Gaimard, 1830. Type locality Tonga-Tabu.

Pteropus keraudrenii Schmeltz, 1864. Misidentification (not *P. keraudren* Quoy and Gaimard, 1824).

Pteropus flavicollis Gray, 1870. Type locality fixed as Moala Island, Fiji, by Andersen (1912).

Pteropus tonganus was described by Quoy and Gaimard (1830) based on specimens obtained by the voyage of the Astrolabe. There are many references in the early literature to *P. keraudreni* (also spelled *keraudrenii* and *keraudrenius*) from Fiji, Samoa, and Tonga, but *Pteropus keraudren* Quoy and Gaimard, 1824 correctly belongs in the synonymy of *Pteropus mariannus*. Andersen (1912) allocated all of the earlier references to the synonymy of *P. tonganus*, but some may in fact refer to *P. samoensis*. *Pteropus flavicollis* Gray (1870) is a junior synonym of *P. tonganus*.

There are several names available for application to populations of this widespread insular species. However, subspecies limits are so poorly understood that it is beyond the scope of this report to attempt to allocate all of them. In our area of interest, Fiji and Samoa, all populations of this species are referable to *P. t. tonganus*. This nominate form extends from Fiji in the west to the Cook Islands in the east (Wodzicki and Felten 1975; Hill and Beckon 1978). Another well-marked and considerably larger subspecies, *P. t. geddiei*, is found from New Caledonia north to Rennell Island and the Santa Cruz Islands (Wodzicki and Felten 1981). The westernmost population is *P. t. basilis-*

cus on Karkar Island, off the coast of New Guinea (Koopman 1979).

Pteropus tonganus is known from all of the major islands in both American and Western Samoa (Andersen 1912; Sanborn 1931; Cox 1983). We found them on Tutuila, 'Aunu'u, Ofu, Olosega, Ta'u, Savai'i, and 'Upolu. They are also found on many small offshore islets. Amerson et al. (1982) reported them from Nu'utele Islet west of Ofu. In Western Samoa, they have been found on Apolima Island and observed feeding on Manono Island.

Pteropus tonganus is known from several islands in Fiji—Viti Levu, Vanua Levu, Taveuni, Ovalau, Moala, Totoya—and probably occurs on many more. We surveyed only on the largest island, Viti Levu.

Description and Morphology

Size

Andersen (1912) noted that when two or more species of *Pteropus* are in sympatry, they generally differ conspicuously in size. This is not true for *P. samoensis* and *P. tonganus*. Andersen (1912) listed forearm lengths of 139–150 mm for *P. t. tonganus* and 140–149 mm for *P. s. samoensis*. Wodzicki and Felten (1975) listed 133–150 mm (average 141 mm) for *P. t. tonganus*, 125–143 mm (average 138 mm) for *P. s. samoensis*, and 120–135 mm (average 135 mm) for *P. s. nawaiensis*. Eleven *P. t. tonganus* in the National Museum of Natural History measured 114–139 mm (average 127 mm), and seven *P. s. samoensis* measured 136–145 mm (average 141 mm).

The wingspans of both species are about the same. Although Cox (1983) stated that *P. samoensis* "is much larger than *P. tonganus* and may prove to be the largest bat known to science with a wing span approaching 2 m (Peale 1848; Anderson [sic] 1912)," we have found no evidence to indicate that *P. samoensis* reaches this size. In fact, Peale (1848) reported the "extent of wings 38 1/2 inches," or 98 cm for a female. Andersen (1912) gave no wingspan measurements. Cassin (1858) gave the wingspan of a male as 40 inches (102 cm). We measured two adult female *P. samoensis* with wings tightly outstretched— each had a wingspan of 122 cm, and an adult male *P. tonganus* had a wingspan of 125 cm.

The skull and dentition differ in several ways between the two species. The rostrum of *P. samoensis* is considerably shorter than in *P. tonganus*. The coronoid process of the mandible is higher, broader, and more steeply ascending in *P. samoensis*. The first pair of lower incisors is much smaller than the second pair in both species, but the disproportion is much greater in *P. samoensis*. The first premolars, both upper and lower, are reduced and peglike in both species, but are a bit more substantial in *P. samoensis*.

Pelage

The body color of *P. samoensis* is brown, darker in the nominate form than in *P. s. nawaiensis*, sometimes with a rusty tinge, sprinkled with grayish white hairs (Figs. 5–7). The mantle is rusty brown, chestnut, or tawny, and the crown varies from buff to silvery gray. The face is sometimes

Fig. 5. Head of *Pteropus samoensis*. Note the pale color of the crown, the brownish neck, and the relatively long shaggy fur.

Fig. 6. Dorsal view of *Pteropus samoensis*. Note the buffy crown, the rusty brown collar, the dark brown back, and the long fur.

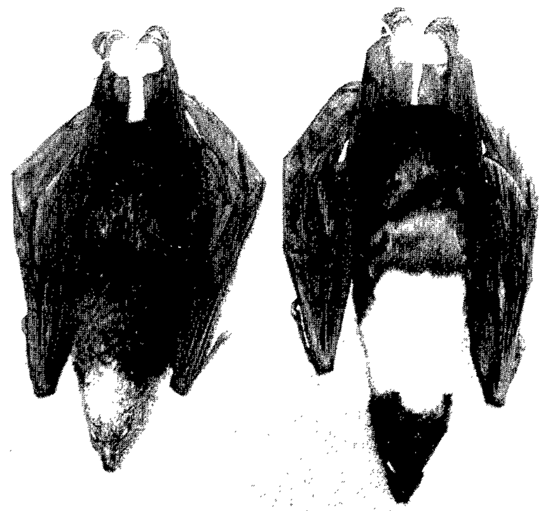

Fig. 7. *Pteropus samoensis* (*left*) and *P. tonganus* (*right*). Note the distinct contrast in crown and mantle color between the two species.

distinctly gray. Wing membranes are dark brown to black.

In *P. tonganus*, the body is blackish or seal-brown, slightly darker and glossy on the dorsum (Fig. 7). The mantle varies from buffy to a very pale cream— buff, and the crown is brownish, similar to the back color. The pale mantle of *P. tonganus* is characteristic of both young and adult bats (Cox 1983). The wing membranes are dark brown to black.

The fur is longer in *P. samoensis* than in *P. tonganus*. In *P. tonganus*, the longest hairs of the back are 10–13 mm; of the mantle, 12–13 mm in males and 16–17 mm in females; and of the belly, 13–15 mm (Andersen 1912). *Pteropus samoensis* has fur about 18 mm long at the middle of the back, 20 mm at the middle of the mantle, and 24 mm at the middle of the belly (Andersen 1912). The slightly shorter fur of *P. tonganus* imparts a glossy appearance to the pelage (Fig. 7). *Pteropus samoensis*, with its longer fur, has a distinctly shaggy appearance, especially when in hand (Figs. 5–6).

Field Identification

Several behavioral and morphological features separate *P. samoensis* and *P. tonganus* in the field, and with binoculars, the experienced observer can identify the two species at distances up to 1–2 km. Under optimal viewing conditions the color of the upperparts serves to clearly separate the two species (Fig. 7). In *P. tonganus* the mantle is pale, sometimes nearly white. There is a distinct con-

trast between the pale mantle and dark back. The crown of the head is dark and contrasts with the paler mantle. In *P. samoensis*, the mantle is a rusty brown; there is usually only minor contrast between it and the brownish back. The buff or silver-gray crown is paler than the mantle, just the reverse of the color scheme in *P. tonganus*. Optimally, an animal should be viewed from above to determine mantle color; however, the color of the mantle extends down the sides of the neck and can often be discerned when the animal is viewed clearly from the side. Several other features visible at close range can be used to aid in separating the two species. The snout is blunt in *P. samoensis* but more pointed in *P. tonganus*. The facial color usually is grayish in *P. samoensis* and dark brown or black in *P. tonganus*.

There is considerable variation in mantle color in both species. The palest mantles of *P. samoensis* approach the shade of the darkest mantles of *P. tonganus*. We also noted variation in crown color of *P. samoensis*. We observed several that had silvery gray crowns, with the grizzly, nearly white color of the crown extending down and around the face. In contrast, others had only a small buffy patch in an otherwise brownish crown and face.

At a distance, the shape of the wings and body, speed and depth of wingbeats, overall color, and habits distinguish the two species. *Pteropus samoensis* has a distinctly stumpier, broader-winged, darker, and often larger appearance than does *P. tonganus* (Figs. 8–10). Though in the hand *P. tonganus* is blacker-bodied than *P. samoensis*, in

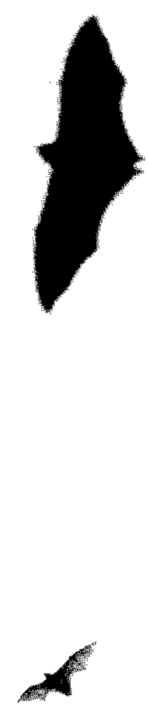

Fig. 8. *Pteropus samoensis* (*upper*) and *P. tonganus* (*lower*) flying at a distance. *Pteropus samoensis* has a dark, triangular shape, a broad appearance to the wings, no deep indentations on the trailing edge of the wings, and a "stump-tailed" appearance. *Pteropus tonganus* has narrow-looking wings, a "tailed" appearance, deep indentations on the trailing edge of the wings, and an overall lighter color. Wingbeats of *P. samoensis* are shallower and slower than those of *P. tonganus*.

Fig. 9. Close view of *Pteropus samoensis* in flight. Note the dark, triangular shape, the broad wings without deep indentations on the trailing edge, and the stump-tailed appearance.

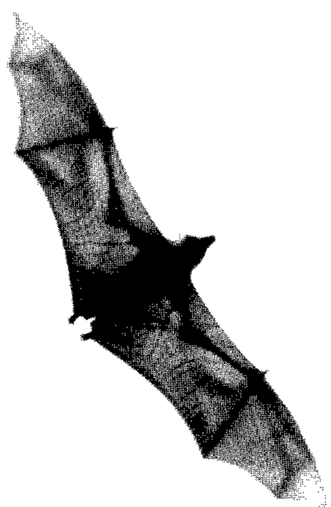

Fig. 10. Close view of *Pteropus tonganus* in flight. Wings appear longer and narrower than in *P. samoensis*. Also notice the pointed nose. This individual is flaring away from the observer and thus does not have the deep indentations on the trailing edge of the wings, nor a distinct "tailed" appearance. A hint of the pale mantle can be seen on the right side of the neck.

the air *P. samoensis* often appears darker than *P. tonganus*. *Pteropus samoensis nawaiensis*, is distinctly paler in appearance in flight than *P. tonganus*. This is particularly noticeable in *P. s. nawaiensis*. The wings of *P. samoensis* typically exhibit a full trailing edge without deep indentations. In *P. tonganus*, the wings appear narrower and have distinct indentations on the trailing edge. *Pteropus samoensis* has a tail-less or stump-tailed appearance, whereas *P. tonganus* appears to have a tail (actually the feet extending to the rear, past the wing membranes). The overall shape of *P. samoensis* in flight is triangular, whereas that of *P. tonganus* is more of a cross. A cautionary note, when flaring, *P. tonganus* has a broad-winged shape similar to *P. samoensis*, and when gliding in a steep descent, *P. samoensis* has the deep indentations on the trailing edge of the wings, much like *P. tonganus*.

Peale (1848) gave a good description of the habits of *Pteropus* in general: "The Pteropi are all more or less gregarious; most active in twilight: and when at rest, hang from the branches of trees with their heads downwards, using their wings as cloaks to shelter their bodies from the wind, rain, and sun; when they fly, as they have no interfemoral membranes, they hold the two hind feet together, which makes them appear to have a tail; they climb with great facility along the under side of the branches, and are very destructive to both wild and cultivated fruits, as they taste and reject until the ripest and best is found; but we never heard them accused of destroying animal life." Later (1848), in the original description of *P. sa-*

moensis, he noted: "It is the least gregarious, and most diurnal, in habits, of any of the genus which we saw; they are frequently abroad at noonday, and fly with the two hind feet together, which makes them appear to have tails." As a comparative trait, this tailed appearance is more applicable to *P. tonganus* than to *P. samoensis* (Fig. 8). Because Peale was not aware that he was observing two species of bats in Samoa, he may have noticed this feature in *P. tonganus* and then mistakenly attributed it to *P. samoensis*.

Wingbeats and flying habits differ between the two species. In Samoa, *P. samoensis* has slow, shallow wingbeats, and commonly soars. In such instances, it resembles a large, soaring hawk (Cox 1983). The wingbeats of *P. tonganus* are faster and deeper; individuals sometimes wheel about, especially when descending from upper ridges. At such times, *P. tonganus* resembles a large, wheeling seabird rather than a bat. Occasionally, when *P. samoensis* is frightened or flushed, it may fly with deep, fast wingbeats similar to those of *P. tonganus*. Interestingly, we never saw *P. s. nawaiensis* soaring in Fiji. Just as Cox (1983) suggested that the lack of predatory birds in Samoa may have fostered the habit there, the presence of the Peregrine Falcon (*Falco peregrinus*) in Fiji may have selected against it.

Habitat use by the two species differs and can sometimes be used as an identification clue but not a reliable indicator, because both species often use the same areas. In general, *P. samoensis* remains in or near native forest and does not venture out into agricultural forests as often as does *P. tonganus*. Frequently sighted in native forest or in adjacent mixed agricultural forest, *P. samoensis* is sometimes found well away from native forest and even in villages. *Pteropus tonganus* commonly roosts in native forest and also forages in it, but it feeds extensively in agricultural forest and in villages and towns.

There is a general pattern of segregation of the two species by activity period and by gregariousness, but again, these are only clues to identification and not distinctive field traits. In most cases, single bats flying during the day or roosting by themselves are *P. samoensis*. Virtually all the solitary roosting bats we found, that could be identified, were *P. samoensis*. Bats moving along a flyway in large numbers in the early morning or at dusk are invariably *P. tonganus*, although a few *P. samoensis* occasionally fly among these groups. We recognized that large groups of bats (more than a dozen) flying about during the day were *P. tonganus*. These were generally individuals that had been disturbed and flushed from a colony or, in the late afternoon, were leaving a colony to feed.

Habits and Ecology

Social Organization

Pteropus samoensis is a solitary species that roosts individually or in pairs (Pernetta and Watling 1978; Cox 1983). The great majority of our observations were of single bats, though loose concentrations of up to a dozen individuals were sometimes observed at feeding sites. On Savai'i, we discovered an exceptional site where we counted as many as 41 bats during a single ½-h census period and saw 9 bats hanging, well spaced, in the same tree. We noticed little interaction between individuals, though on at least two occasions we heard *P. samoensis* squabbling among themselves. Occasionally, we saw bat chases and saw one individual following another. We did not collect data on *P. samoensis* that would confirm or reject pair bonding as suggested by Cox (1983).

Pteropus tonganus is a social species that roosts in colonies, often with several hundred bats in a single tree (Pernetta and Watling 1978; Cox 1983). Amerson et al. (1982) located colonies in American Samoa, some numbering in the thousands. All the *P. tonganus* that we found roosting were in colonies. The largest colony was on Viti Levu in Fiji, where we estimated at least 7,000 individuals spread through at least 11 large trees in undisturbed native forest within a few miles of the outskirts of Suva. The only suggestion that *P. tonganus* might roost singly is that of Wodzicki and Felten (1975): "On Niue *P. tonganus* has been reported to roost either singly, in pairs, or in larger groups." Presumably, these reports are by local inhabitants, as we know of no published records. Actually, only seven specimens are known from Niue (some 500 km south of Samoa), and five of those are immature (Wodzicki and Felten 1975; Hill 1979). If there are *Pteropus* roosting singly or in pairs on Niue, the possibility remains that they are *P. samoensis*, as yet unknown from that island.

We did not notice interactions between *P. samoensis* and *P. tonganus*. I. Gurr (in correspondence) found a tree containing both species on Tutuila. Colonies we observed contained all *P. tonganus*, although on several occasions we saw indi-

vidual *P. samoensis* flying in the immediate vicinity of a colony. Away from colonies, we commonly saw the two species flying and foraging in the same general area. Also, there were occasionally a few *P. samoensis* flying among the *P. tonganus* moving along a large flyway.

Habitat

We found *P. samoensis* to be more widely distributed than reported by Cox (1983), who considered the species to be restricted to undisturbed rain forest. We found *P. samoensis* in primary and secondary native forest, in agricultural forest, and sometimes in villages. All types of native forest are used, including cloud forest and montane scrub. We observed *P. samoensis* from the seacoast to the highest elevations we visited (900 m on Savai'i). On Ta'u, we saw an individual using cloud forest near the top of the island (about 800 m elevation). However, the cloud forest on the higher elevations of Ta'u appears to provide only marginal habitat compared to mature rain forest at lower elevations. On Tutuila, Ofu, and Olosega, which are lower than Ta'u or Savai'i, *P. samoensis* used higher and lower elevations.

In plantation areas, diverse agricultural forest with a variety of food trees is preferred. *Pteropus samoensis* is not attracted to extensive tracts of homogeneous agricultural forest, such as large coconut plantations. On 'Upolu, *P. samoensis* is found primarily in the upland interior forest rather than along the coastal plains, which have been largely converted to coconut plantations. On Savai'i, which has native forest along much of the lowlands, the species is found at lower and higher elevations.

In the interior of 'Upolu, we occasionally found *P. samoensis* in relatively open pastureland, where individuals roosted high in massive *Ficus* trees. Pernetta and Watling (1978) suggested that *P. samoensis* feeds in more open habitats than does *P. tonganus* in Fiji, but we saw none in such habitats during two trips across Viti Levu in an open vehicle. All of our observations of *P. s. nawaiensis* were in relatively dense forest.

We spotted *P. tonganus* roosting in primary or secondary forest at inaccessible sites where colonies were protected from human intrusion. Likewise, Amerson et al. (1982) uncovered colonies located in primary or secondary forest, usually in inaccessible areas near mountaintops, on islets, or near cliffs. From these colonies, *P. tonganus* disperses to forage in agricultural or secondary forests (Cox 1983). We commonly recorded *P. tonganus* foraging in agricultural forest, in or around villages. Nightly, large numbers of *P. tonganus* dispersed to forage over the Tafuna plains, Tutuila. Even well-developed residential areas were used by *P. tonganus*. We saw and heard *P. tonganus* squabbling at night in Suva on Viti Levu, Fiji; Apia on 'Upolu, Western Samoa; Asau on Savai'i, Western Samoa; and in Pago Pago on Tutuila in American Samoa. Throughout Fiji and Samoa, we found that we could see *P. tonganus* flying to and from roosting sites at dawn and dusk from many vantage points.

Activity Patterns

Cox (1983) reported *P. samoensis* to be almost strictly diurnal, the peak of activity occurring between 1100 and 1400 h. We observed this species during all of the daylight hours but found it to be most active in the morning until about 1000 h and in the afternoon after 1400 h, with a slight lull in activity around midday. Most census data are difficult to analyze for activity patterns because of variation between sites and seasons. We have two small data sets that address the question directly, and both support a general activity pattern of a slow increase in activity to a midmorning peak around 0900 or 1000 h, a midday lull, and then a steady increase to an overall peak in late afternoon from 1500 to 1700 h.

The first of these (Fig. 11) we gathered on 28 July 1989, by making half-hour counts beginning every hour on the hour at a site on Savai'i where we had recorded the highest density known to us (41 in a ½-h census). We gathered the second data set (Fig. 12) from 30 July to 1 August 1989, by making ½-h counts from the summit of Mt. Vaea on Savai'i. We made from one to four counts during each daylight hour, and the data in Fig. 12 represent the average number seen. In contrast, we did eight counts from the runway on Ofu, American Samoa, beginning at 0700 h, and recorded only a single *P. samoensis* in each count. From the foraging pattern exhibited there, we suspect it was the same bat using the area all day.

Andersen (1912), referring to the fruit bat population in Tonga, wrote, "Like many other species of the genus, *P. t. tonganus* appears sometimes on the wing in the early afternoon in full sunlight, but as dusk comes on it becomes more and more plentiful, and it is probably only those accidentally disturbed or specially driven by hunger that come out before dusk." We found that *P.*

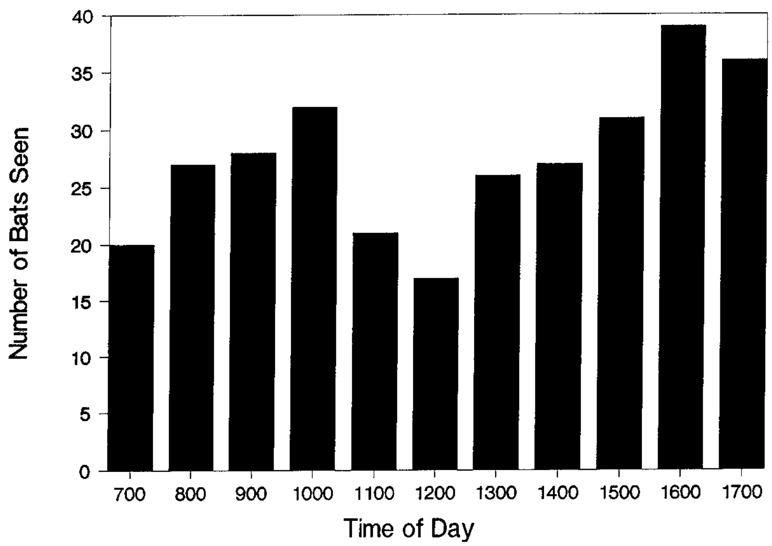

Fig. 11. Number of bats seen in each of eleven 30-min counts at Via'a'ata, Savai'i, Western Samoa on 28 July 1989.

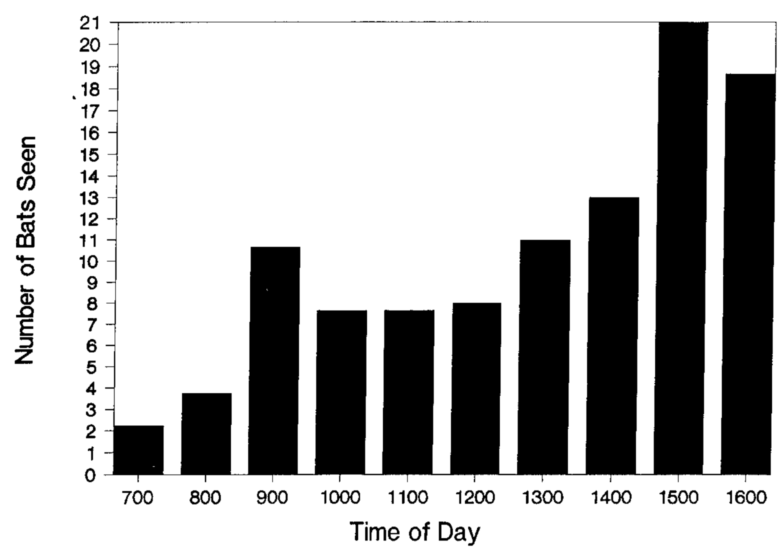

Fig. 12. Average number of bats seen per 30-min count during each hour of the day at Mt. Vaea. Total number of counts was 28.

tonganus mostly remained in colonies during the day, departing at dusk to forage at night. We saw and heard individuals throughout the night and saw bats returning to colonies at daybreak. *Pteropus tonganus* often flies considerable distances as it moves back and forth between roosts and feeding sites. Bats sometimes fly between islands, and we observed one individual flying from 'Aunu'u to Tutuila, a distance of 2 km. On Tutuila at dusk, we regularly saw large numbers move from the mountains down onto the Tafuna Plains. On the south coast of 'Upolu, large numbers were flying across the road near Togitogiga at dusk, presumably from a colony near the coast or on an offshore islet, possibly Nu'usafe'e. On Savai'i, we saw a large flyway of *P. tonganus* moving across the Tafua Road at 0830–0930 h. We believe these bats were returning to a colony after foraging during the night. We watched the large colony near Suva on Viti Levu, Fiji, disperse at dusk and return at dawn on several days.

We noticed some differences in activity periods for *P. tonganus* on different islands. On Tutuila, 'Upolu, Savai'i, and Viti Levu, *P. tonganus* was seldom seen flying in large numbers during the day unless a colony had been disturbed or unless bats remained in areas relatively undisturbed by people. Individuals began entering foraging areas in large numbers shortly after dusk (about 1830 h). On 'Aunu'u and Olosega, *P. tonganus* became active earlier in the afternoon. On these islands, bats were seen leaving colonies to

begin foraging as early as 1530 h. We attribute this behavioral difference to varying intensities of hunting pressure and other human disturbance. On the larger islands, human disturbance is high, and *P. tonganus* forages primarily under the cover of darkness. On 'Aunu'u and Olosega, human disturbance is low, and bats are able to forage with minimal risk during daylight.

Foods and Feeding

The genus *Pteropus* feeds on fruit, nectar, pollen, and, rarely, other plant material (Marshall 1983). Fruit bats are known to be important pollinators and seed dispersers in tropical forest ecosystems. In Fiji and Samoa, both species feed on a variety of foods in native and agricultural forest. Although *P. tonganus* seems to forage primarily in agricultural forest, whereas *P. samoensis* forages more in native forest. The two species undoubtedly have different feeding niches and ecological strategies, but these have yet to be studied. Possibly, *P. samoensis* focuses on a variety of limited food sources over the year, rather than on an abundant, specific food crop like breadfruit, which may be the strategy of *P. tonganus*.

Cox (1983) observed *P. samoensis* taking the fruit of *Cupaniopsis samoensis* and the inflorescence of *Freycinetia reineckei*, and he obtained local reports of this species feeding on fruits of various *Ficus* species and *Dysoxylum maota*. Kiso So'oto, Edwin Seui, and Fia Tiapula (American Samoa Office of Marine and Wildlife Resources 1988, unpublished report) compiled a list of plants used by *P. samoensis* that includes *Myristica fatua, Persea americana, Carica papaya, Musa paradisiaca, Inocarpus fagiferus, Psidium guajava, Aglaia samoensis, Canarium vitiense, Mangifera indica, Terminalia richii, Cananga odorata, Morinda citrifolia, Artocarpus altilis, Spondias dulcis, Cocos nucifera, Barringtonia asiatica, Grewia crenata, Erythrina variegata,* and *Syzygium* sp.

We recorded *P. samoensis* foraging on various fruits and flowers. Individuals were attracted to ripening breadfruit in agricultural forest near Amalau, Tutuila. At dusk, a large number of *P. tonganus* also moved into this general area. Both species could be seen landing in breadfruit trees and carrying breadfruit pieces in their mouths. On Ofu, we observed a single *P. samoensis* roosting alongside a partly eaten breadfruit. We also saw *P. samoensis* landing in breadfruit trees on Olosega and Ta'u. At Leone, Tutuila, two female *P. samoensis* were shot by hunters as they fed on the flowers of *Cananga odorata*. In the same area on the previous evening, a male *P. samoensis* was taken as it fed on the flowers of *Ceiba pentandra*. We watched 6–10 scattered individuals foraging on the northwest slope of Pioa Mountain, Tutuila, at 360–430 m. Bats seemed to be particularly attracted to scrubby *Pandanus* trees, in which they landed and moved about with agility as if searching for food. We saw a single *P. s. nawaiensis* do the same thing on Viti Levu, Fiji. They may be eating flower or leaf buds from the centers of the terminal rosettes of these plants.

Cox (1983) listed breadfruit, papayas, mangos, bananas, *Syzygium jambos*, and *Ceiba pentandra* flowers as foods taken by *P. tonganus*. We observed *P. tonganus* foraging on breadfruit and on the flowers of *Ceiba pentandra, Cananga odorata, Musa paradisiaca,* and *Cocos nucifera*. At Fagamalo, Tutuila, we recorded *P. tonganus* feeding on the thin outer flesh of *Callophyllum inophyllum* fruits. We saw individuals feeding on coconut flowers on Viti Levu, Savai'i, and 'Aunu'u.

There are a number of reports of depredation problems posed by fruit bats to agricultural crops (Peale 1848; Cassin 1858; Whitmee 1875; Nicoll 1908; Amerson et al. 1982; Cox 1983). Many types of fruit are said to be taken, but breadfruit is the crop mentioned most often. Most of this damage is probably attributable to the more abundant *P. tonganus*.

Reproductive Cycle

Details of the annual reproductive cycle are unknown for both species. We noted several adult female *P. samoensis* carrying young in June, July, and August. Reports from biologists of the American Samoa Office of Marine and Wildlife Resources (K. So'oto and M. Ulugulu, personal communication) suggest that young are born throughout the year. The general pattern for pteropodids is one young per year, with one or two seasonal peaks (Martin et al. 1987).

On several occasions, both on Savai'i and on Tutuila, we watched two *P. samoensis* following each other, flying the same path, and wheeling together. Twice on Tutuila, we saw the animals grapple briefly in flight before separating and continuing to fly. This suggested some type of courtship behavior, but we were unable to sex the animals.

Status

Former Accounts

There is little reliable information regarding the past status of either species of fruit bat in Fiji and Samoa, most accounts refer collectively to both species. Cassin (1858), citing a journal by Dr. Pickering, recorded that bats were common everywhere in the Manu'a Islands, on Tutuila, 'Upolu, and Savai'i. Whitmee (1875) wrote, "*Pteropus* is very common in Samoa." Nicoll (1908) stated that many bats were "seen flying about over the trees even in broad daylight, while at dusk so many of these huge bats came down from the high forests, that we judged there must be a large colony of them at no great distance from Pago-Pago." According to Peale (1848), "We found a species of bat very common at the Feejee Islands, which agrees with the descriptions above quoted; the native name is 'Beka,' which is also the native name of a closely-allied species inhabiting the island of Tongatabu." Many of the bats observed in these accounts were probably the more numerous of the two species, *P. tonganus*.

Amerson et al. (1982) attempted to quantify the number of bats found in American Samoa, but they, also, were unaware that two species were present. Based on counts made at study plots, and on the roadside they estimated a total population of 140,000 in American Samoa. Their estimate most likely refers primarily to *P. tonganus*, but the methods used in determining density are not clearly described, and it is not possible to duplicate their study. However, based on our knowledge of forest bird densities in American Samoa, we commonly found their estimates to be up to 10 times higher than those obtained during a 1986 FWS survey.

Cox (1983) reported that *P. tonganus* was found in large colonies, was considered a pest in agricultural areas, and did not seem to have been severely affected by hunting for local consumption. Conversely, he regarded *P. samoensis* as rare and endangered because of loss of forests and the opportunistic shooting of bats by pigeon hunters. He was only able to locate a single breeding pair on Tutuila and only a single individual on Ta'u. He estimated that, in Western Samoa, there were less than 50 remaining bats on 'Upolu, while Savai'i possibly supported a larger population.

Survey Results

Pteropus samoensis

In 1986, we established and conducted 30-min counts from 53 stations: 29 in American Samoa and 24 in Western Samoa (Table 1; Figs. 1–4). In 1989, we resurveyed 50 of those at about the same time of year and day. The numbers recorded during

Table 1. Pteropus *recorded at 50 stations in Samoa, 1986 and 1989. Counts (30-min) were conducted on Tutuila (21 sites), Ofu (3), Olosenga (3), Ta'u (2), 'Upolu (17), and Savai'i (4).*

Station	Date	Time (h)	*P. samoensis*	*P. tonganus*	Unidentified	Total
Tutuila						
Leone	3 July 1986	1645	3	1	0	4
	6 August 1989	1652	5	1	2	8
Asili	3 July 1986	1726	10	17	2	29
	6 August 1989	1608	5	1	2	8
Tuigaava	3 July 1986	1700	3	0	2	5
	4 August 1989	1714	9	0	0	9
Fagalii	3 July 1986	1742	2	6	6	14
	4 August 1989	1636	8	2	1	11
Ogefao	7 July 1986	0850	2	0	1	3
	5 August 1989	0934	4	1	0	5
Onenoa	7 July 1986	0937	5	0	0	5
	5 August 1989	1013	4	5	1	10
Tula	7 July 1986	1020	0	0	0	0
	5 August 1989	0848	4	4	1	9
Masefau	8 July 1986	0800	3	0	0	3
	5 August 1989	1545	4	0	0	4
Talaloa	8 July 1986	0843	2	1	0	3
	5 August 1989	1509	7	1	1	9
Masausi	8 July 1986	0940	1	0	0	1
	5 August 1989	1627	7	8	0	15
Fagaitua	8 July 1986	1028	0	0	0	0

Table 1. *Continued.*

Station	Date	Time (h)	*P. samoensis*	*P. tonganus*	Unidentified	Total
	6 August 1989	0742	3	3	2	8
Nu'uuli	12 July 1986	1425	7	7	3	17
	6 August 1989	1519	7	10	4	21
Vaitanoa	12 July 1986	1515	5	5	1	11
	13 August 1989	0839	2	0	0	2
Fagaalu	12 July 1986	1604	0	0	0	0
	7 August 1989	0826	0	0	0	0
Faganeanea	12 July 1986	1647	7	11	3	21
	6 August 1989	1415	8	0	0	8
Sagamea	12 July 1986	1727	7	8	2	17
	6 August 1989	1453	7	0	0	7
Alega	12 July 1986	1448	4	0	1	5
	6 August 1989	0859	0	9	3	12
Amaua	12 July 1986	1526	1	0	1	2
	6 August 1989	0821	4	2	0	6
Alofau	12 July 1986	1601	3	2	2	7
	5 August 1989	1706	4	8	1	13
Pioa Mt.	12 July 1986	1652	7	0	1	8
	6 August 1989	0949	2	0	0	2
Maugaloa	12 July 1986	1623	10	4	1	15
	6 August 1989	1019	7	0	0	7
Tutuila Totals						
21 Counts	1986		82	62	26	170
21 Counts	1989		101	55	18	174
Ofu						
Runway	17 July 1986	1520	2	0	0	2
	7 August 1989	1608	2	0	1	3
Toaga	17 July 1986	1631	3	2	0	5
	7 August 1989	1654	2	0	1	3
Leolo	17 July 1986	1721	1	4	1	6
	8 August 1989	1552	1	0	0	1
Olosega						
Tumatolu	17 July 1986	1535	3	10	0	13
	8 August 1989	0814	8	0	0	8
Sili	17 July 1986	1616	6	15	0	21
	8 August 1989	0904	5	0	0	5
Olosega	17 July 1986	1717	9	27	0	36
	8 August 1989	1446	1	0	1	2
Ta'u						
Lepula	23 July 1986	1449	5	17	0	22
	10 August 1989	0840	3	2	2	7
Letula	23 July 1986	1453	1	12	1	14
	9 August 1989	1715	1	10	0	11
Manu'a Totals						
8 Counts	1986		30	87	2	119
8 Counts	1989		23	12	5	40
American Samoa Totals						
29 Counts	1986		112	149	28	289
29 Counts	1989		124	77	23	214
'Upolu						
Mt. Vaea	30 July 1986	1632	2	0	0	2
	3 August 1989	1704	1	0	0	1
Tiavi	30 July 1986	1643	7	0	1	8
	3 August 1989	1536	0	0	0	0
Afiamalu	30 July 1986	1734	3	2	1	6
	3 August 1989	1613	2	0	2	4
Falefa	31 July 1986	1622	0	0	1	1
	26 July 1989	0654	0	0	0	0

Table 1. *Continued.*

Station	Date	Time (h)	*P. samoensis*	*P. tonganus*	Unidentified	Total
Falevao	31 July 1986	1609	0	0	0	0
	26 July 1989	1716	3	0	0	3
Lemafa	31 July 1986	1651	7	1	0	8
	26 July 1989	0750	3	0	0	3
Mt. Poutavai	31 July 1986	1730	5	0	1	6
	26 July 1989	0826	1	0	0	1
Mt. Tafua N.	1 August 1986	1455	0	0	4	4
	2 August 1989	1618	1	0	3	4
Mt. Tafua S.	1 August 1986	1442	4	0	0	4
	2 August 1989	1536	2	0	2	4
Faleaseela	1 August 1986	1555	10	1	1	12
	25 July 1989	1600	5	0	0	5
Mt. Tiatala	2 August 1986	1555	4	0	0	4
	3 August 1989	1012	0	0	0	0
Mt. Savaii	2 August 1986	1638	6	0	0	6
	3 August 1989	0820	0	0	0	0
Vaipu	2 August 1986	1730	9	0	0	9
	26 July 1989	0913	1	0	0	1
Richardson-1	2 August 1986	1550	8	0	0	8
	3 August 1989	0935	1	0	0	1
Richardson-2	2 August 1989	1637	9	0	2	11
	3 August 1989	0855	0	0	0	0
Richardson-3	2 August 1986	1725	7	0	1	8
	3 August 1989	1100	1	0	1	2
Tiavi Falls	5 August 1989	1702	8	0	0	8
	3 August 1986	1457	2	0	0	2
'Upolu Totals						
17 Counts	1986		89	4	12	105
17 Counts	1989		23	0	8	31
Savai'i						
Asau-1,500 m	4 August 1986	1618	9	2	1	12
	29 July 1989	1638	4	0	1	5
Asau-750 m	4 August 1986	1726	5	5	0	10
	29 July 1989	1728	0	0	5	5
Asau-2,250 m	4 August 1986	1630	3	0	1	4
	29 July 1989	1547	3	0	1	4
Mauga	5 August 1986	1607	3	0	0	3
	27 July 1989	1534	0	0	0	0
Savai'i Totals						
4 Counts	1986		20	7	2	29
4 Counts	1989		7	0	7	14
Western Samoa Totals						
21 Counts	1986		109	11	14	134
21 Counts	1989		30	0	15	58
Samoa Grand Totals						
50 Counts	1986		221	160	42	423
50 Counts	1989		154	77	23	267

all counts reflected the number of individuals that were observed rather than the number of sightings actually made, which was usually higher.

We recorded *P. samoensis* on all the major islands visited: Tutuila, Ofu, Olosega, Ta'u, 'Upolu, Savai'i, and Viti Levu. We did not record *P. samoensis* on the small island of 'Aunu'u, although *P. tonganus* was common there. *Pteropus samoensis* was observed on 47 of 53 (89%) counts in 1986, and on 41 of 50 (82%) counts in 1989 (Table 1). An average of 4.4 individuals was recorded per count in 1986, and 3.1 individuals per count in 1989 (Table 2).

One simple way to evaluate the differences between the two data sets is to test the hypothesis that the mean number of individuals per count did not differ between the 2 years. We used student's *t* tests on combined data sets for American and Western Samoa, as well as for individual islands and groups (Table 2). The results led to a rejection of the null hypothesis for the entire data set combined, but an island-by-island examination showed that the difference was entirely attributable to a decline on 'Upolu (Table 2). Differences between the two counts were not significantly different for any of the other islands (Table 2).

The apparent decline on 'Upolu is statistically significant and signals the possibility of serious problems for *P. samoensis* on that island in the near future. Much of the island has been cleared for agriculture, leaving natural forest habitats only on the more inaccessible mountainous areas in the center of the island. Most of our count sites are in some combination of natural and degraded or agricultural forest, which may represent marginal habitat for this species. For that reason, we caution against the use of our survey data to represent actual population sizes on 'Upolu.

The situation on Savai'i remains mostly unknown, because of the physical features of the island and the difficulty in penetrating to the central undisturbed areas where *P. samoensis* would be expected to be most numerous. Savai'i is large enough that the central mountainous areas, where relief is sharp, are separated from the island-encircling access road by considerable expanses of gradual slopes that do not afford the ideal field of view for visual counts. The six sites we surveyed in 1986 were hastily chosen and not representative of the island in general. Three were coastal, and three were mountainous, but by 1989, all had changed

Table 2. *Statistical evaluation of 1986 and 1989 census data for* Pteropus samoensis. *Probabilities are from* t *tests of equality of means, and values greater than 0.05 indicate no significant difference.*

Location/ Date	Number of bats	Number of counts	Standard mean	Error	*t* value	Probability
Tutuila						
1986	82	21	3.9	0.676		
1989	101	21	4.8	0.559	1.032	1.00
Manu'a						
1986	30	8	3.8	0.977		
1989	23	8	2.9	0.875	0.667	1.00
American Samoa						
1986	112	29	3.9	0.550		
1989	124	29	4.3	0.491	0.561	1.00
'Upolu						
1986	91	18	5.2	0.807		
1989	23	17	1.4	0.331	4.451	0.00
Savai'i						
1986	29	6	4.8	1.414		
1989	7	4	1.8	1.031	1.857	0.11
Western Samoa						
1986	120	24	5.0	0.692		
1989	30	21	1.4	0.321	4.932	0.00
Samoa Total						
1986	232	53	4.4	0.437		
1989	154	50	3.1	0.371	2.336	0.02

because of growth of roadside vegetation so as to further limit their usefulness. Although we did manage to resurvey four of the six, we had to shift our vantage points to such an extent that we do not believe the data are strictly comparable.

In 1989, we did find several other sites that might be used for visual counts. In the lowlands, 4 such sites that we censused yielded a total of 13 *P. samoensis*, 1 *P. tonganus*, and 10 unidentified animals that we believed were most likely *P. samoensis*. Those numbers are indicative of our general impression of the numbers of *P. samoensis* seen while exploring several roads through the lowlands of Savai'i. Bats are much more obvious on Savai'i than on 'Upolu.

We located a site on the Vai'a'ata Road on the eastern end of Savai'i that afforded a view across a medium-sized taro field to a rather sharp forest edge, with the forest continuing back on a gradually rising slope to a ridge about 2 km distant. It did not look like particularly good *P. samoensis* habitat, but it seemed to be representative and offered a vantage point, so we did a count at 1705 h on 27 August and recorded a remarkable 41 bats, the largest count we have made to date.

We devoted the following day to making 11 additional counts there, 1 per hour on the hour, beginning at 0700 h and ending at 1730 h. The results (Fig. 11) confirmed that this was an extraordinary site: the lowest number we counted was 17 (at 1200 h), and the highest was 39 (at 1600 h). The nature of the site allowed us to see many individuals roosting simultaneously, another unusual occurrence. The number roosting during each count period ranged from 4 to 17. Most were solitary, although a single tree held as many as nine individuals during some count periods. The number flying, apparently foraging, ranged from 10 to 29. The total number for the day was 298. This of course does not represent 298 separate individuals, but rather some number between 39 and 298. At this site, we had repeats of the same individuals during successive counts.

We discovered a second excellent vantage point for watching *P. samoensis* alongside the radio tower on the top of Mt. Vaea near the western end of Savai'i. There, we divided the 360° field of view into three approximately equal areas, and conducted 26 counts at various times of the day from 0700 to 1750 h on 3 consecutive days beginning 30 July (Fig. 12). Those counts yielded a total of 227 bats. Once again, this represents some unknown number of individuals between 23 (the highest number recorded during any one count) and 227. However, the behavior of most animals at this site suggested to us that we were actually counting mostly different animals in each count period.

At that site, the bats could be divided into three basic groups, based on activity. Most were moving inland, uphill, from north to south, gaining altitude by soaring on thermals, and eventually sustaining flapping flight until out of sight. The second most common segment was moving in the opposite direction, soaring much lower and more rapidly just above the canopy, and working their way downhill until out of sight. The third cohort included individuals foraging in our immediate vicinity; we could see them circle repeatedly and occasionally alight in nearby trees.

After watching those bats for 3 days, we ascertained they use thermals to gain sufficient altitude to make their way inland to the highest peaks in the most energetically favorable manner. Then, they may forage gradually down the mountain slopes, using the terrain to cover maximum territory with minimal outlay of energy for flight. This might help to explain the evolution of soaring behavior in this subspecies, a seemingly useless trait in a frugivore.

Considerably more data exist for American Samoa to fill the gap between 1986 and 1989. Biologists from the American Samoa Office of Marine and Wildlife Resources conducted surveys similar to ours at most of our sites in June and December 1987 and in January, May, and August 1988. In all but December 1987, two complete sets of counts were made (Table 3).

To compare all the results, we calculated the mean number of bats per count and multiplied by 21, the number of sites in our 1986 and 1989 surveys. This allowed us to use all surveys, which varied in number of counts from 17 to 50. The totals ranged from a low of 47 (2.24 per count) in May 1988 to a high of 105 (5 per count) in December 1987 (Table 3). The mean was 74.2, variance 349, standard deviation 18.7, and standard error 5.6. The 95% confidence limits were 61.3–87.1, and the coefficient of variation was 25.

In a variable sequence with no obvious trend (such as these data appear to demonstrate), one obvious test is to determine if the data fit a normal distribution. If there is a significant increasing or decreasing trend, the samples should depart from a normal distribution. Thus, the null hypothesis is that the data do not significantly differ from the normal distribution. Two statistics, $g1$ and $g2$,

Table 3. Pteropus samoensis *recorded during 11 surveys on Tutuila, 1986–89. Adjusted total is the mean multiplied by 21, to standardize data to the initial and final surveys. Of the 246 counts, the initial and final 21 were 30-min counts, and all of the intervening ones were 20-min counts.*

Date	Number of bats	Number of counts	Mean	Adjusted total
July 1986	82	21	3.9	82
June 1987	70	20	3.5	74
June 1987	86	20	4.3	90
December 1987	85	17	5.0	105
January 1988	73	25	2.92	61
January 1990	71	25	2.84	60
May 1988	56	25	2.24	47
May 1988	68	25	3.40	71
August 1988	83	25	3.32	70
August 1988	63	24	2.63	55
July 1989	101	21	4.8	101

were applied to test the hypothesis. If the confidence limits for $g1$ and $g2$ bracket zero, one may conclude that the distribution does not depart from normal (Pimental and Smith 1986). The confidence limits for $g1$ are −0.909 to 1.682, and for $g2$, −3.306 to 1.711; hence, we cannot reject the null hypothesis.

A more sensitive test to departures from normality is the Kolmogorov-Smirnov D statistic. It tests the same null hypothesis by examining the single, greatest deviation found between the observed and expected frequencies. To reject the null hypothesis, the D statistic must surpass the critical or adjusted critical value of an a priori level of significance. In this case, the calculated D is 0.14025, well below the adjusted level (0.05) needed to reject the hypothesis. Once again, we may conclude the data do not differ from a normal distribution.

Another way to test the data for trends is to test the null hypothesis that the data represent a random sample. To do so, we evaluated the serial correlation (a two-tailed test) by a C statistic that measures the association between contiguous pairs of observations. If the C statistic is greater than the critical value, the data conform to a trend (i.e., observations increase or decrease in value). For our data, $C = 0.2021 < 0.452$, suggesting a random distribution of samples from a normally distributed population. Therefore, we cannot demonstrate either an increase or decrease in numbers through time, so we may conclude the number of bats has remained roughly the same from 1986 to 1989.

Data are also available for Manu'a from 1987 and 1988 (Table 4). The pattern there may be related to the effects of Typhoon Tusi, which devastated much of the forest in January 1987. If we accept the earliest available data—1986—as the baseline, then the basic pattern is for a decline to about half in 1987, followed by an increase in 1988 and 1989. Residents on Ta'u told us many bats died as a result of the typhoon and subsequent food shortages. However, the numbers recorded in 1988 and 1989 suggest that the populations there are rebounding quickly. To augment the data from our two sites on Ta'u, we also recorded four counts at Lepue Crater on the afternoon of 11 August

Table 4. Pteropus samoensis *recorded during five surveys in Manu'a, 1986–89. Adjusted total is the mean multiplied by 1986 count number, to standardize data to the initial survey. Of the 86 counts, the initial and final ones were 30-min counts and the intervening ones were 20-min counts.*

Location/ date	Number of bats	Number of counts	Mean	Adjusted total
Ofu				
July 1986	6	3	2.0	6
July 1987	3	9	0.3	1
May 1988	13	9	1.4	4
September 1988	12	8	1.5	5
July 1989	5	3	1.7	5
Olosega				
July 1986	18	3	6.0	18
July 1987	33	6	5.5	17
May 1988	19	7	2.7	8
August 1988	29	7	4.1	12
July 1989	14	3	4.7	14
Ta'u				
July 1986	6	2	3.0	6
May 1988	53	10	5.3	11
August 1988	47	10	4.7	9
July 1989	22	6	3.7	7
Ofu-Olosega (combined)				
July 1986	24	6	4.0	24
July 1987	36	15	2.4	14
May 1988	32	16	2.0	12
August 1988	41	15	2.7	16
July 1989	19	6	3.2	19
Manu'a total				
July 1986	30	8	3.8	30
July 1987	36	15	2.4	14
May 1988	85	26	3.3	26
August 1988	88	25	3.5	28
July 1989	41	12	3.4	27

1989. We saw three bats in the ½ h beginning at 1530 h, two at 1600 h, six at 1630 h, and seven during the final ½ h beginning at 1700 h.

There are no previous survey data for *P. samoensis naiwensis* on Fiji, and we were unable to establish a quantitative sampling system there during our short visit in 1989 because of the difference in behavior of this subspecies. The fact that these bats do not soar high above the forest makes them more difficult to census, even though they are diurnal. Because of the dearth of information available, we will briefly summarize our observations, which include those of G. Graham of Bat Conservation International, who joined us for the surveys on Fiji.

On 19 July at 1740 h in the hills above Suva, we watched two bats, one of which hung in a small tree about 35 m from us for 15 min. On 20 July at 0720 h in Colo-I-Suva Forest Park, we watched a bat land in a mahogany tree, where it remained for about 15 min. Later that day (1715 h) we glimpsed a bat flying along just above the treeline around a clearing on a steep slope of undisturbed forest in the Garrick Reserve. On 21 July at 0715 h, one flew over a powerline access road near the large *P. tonganus* colony above Suva. That afternoon, we saw nine different bats foraging in the same general area and along the Wailoku Road. All were flying in and out of the canopy, and occasionally one would land for a short time. On 23 July, we saw one from a powerline tower above the large *P. tonganus* roost, which we were attempting to census.

Later that day, at the Garrick Reserve, we saw six bats during the course of several long transect walks along a forest road and two 30-min site counts. One of the bats landed in a tree nearby, and we attracted its attention by squeaking. It flew low and slowly, making three complete circles over our heads, curiously looking at us. It then flew into a roadside *Pandanus* sp., where it seemed to be foraging in the center of the leaf rosettes. At first we thought it might be drinking, but it later appeared to be chewing on the leaf buds or newly opening shoots.

Pteropus tonganus

This species is much more common than *P. samoensis*, but because it is basically nocturnal and colonies are remote, it can sometimes be less conspicuous than *P. samoensis*. The numbers we observed during our counts (Table 1) are quantifiable and comparable, but we do not believe the data are particularly useful because *P. tonganus* is primarily nocturnal. We made no effort to visit all the *P. tonganus* colonies of which we were aware, but incidentally gathered information while in the field. All the population estimates given here are simply our best guesses. There are probably thousands or tens of thousands of *P. tonganus* on each of the islands of Tutuila, the Manu'as, 'Upolu, and Savai'i. Numbers in Fiji are more likely in the hundreds of thousands. Large, inaccessible colonies are located on the major islands as well as on some of the offshore islets. Even small islands such as 'Aunu'u support colonies of several hundred.

In many areas bats are heard or seen nightly as they move into and feed in agricultural areas. Amerson et al. (1982) found roosts scattered throughout Tutuila and gave locations of colonies on 'Aunu'u, Ofu, Nu'utele (near Ofu), Olosega, and Ta'u. Several of these colonies probably contain more than a thousand bats each. Amerson et al. (1982) reported a colony of thousands at Fagatele Point on Tutuila. On 25 June 1986, we photographed bats flushed from this colony and counted 3,169 in one photograph. This represented only a portion of the bats in the colony, and we estimated the roost to number 5,000. This was one of the largest colonies on Tutuila. We are aware of several other colonies and flyways on Tutuila, and we conservatively estimate the population at 12,000. Recent islandwide counts conducted by the Department of Marine and Wildlife Resources have yielded estimates of 28,000 (± 6,000) in 1987 and 18,000 (± 6,000) in 1988.

Based on our incidental observations of flyways and foraging *P. tonganus* in Western Samoa, we believe that densities are similar to those on Tutuila. We counted 100 in a *Terminalia catappa* tree near Fagefau on Savai'i. We regularly saw and heard them feeding in trees in Apia on 'Upolu. Considering that Western Samoa has nearly 15 times the land area of American Samoa, we believe the population numbers in the tens of thousands on each of 'Upolu and Savai'i. The total population in Samoa is probably over 100,000.

In Fiji, we developed an impression for *P. tonganus* numbers by watching at several sites at dawn and dusk, and counting numbers of individuals passing overhead. On the evening of 18 July, we saw 16 crossing the highway from inland to a mangrove area about 15 km west of Suva, and 3 more were seen in the same area the following morning. On the evening of 19 July, we counted 40 crossing the road in the hills above Suva. On the morning of 20 July, we counted 106 crossing

Princess Road near the Colo-I-Suva Forest Reserve. We saw only a single individual that evening in the Garrick Reserve. On the morning of 21 July, we saw 17 crossing a valley near the large roost above Suva. In addition, we saw and heard *P. tonganus* every night in the city of Suva. They were particularly numerous around the botanic garden, but we also heard them nightly in coconut trees outside our hotel.

We attempted to estimate the size of the large colony we located in the forest above Suva. The colony was spread over at least 11 large trees, and we could not find a site from which the entire colony was visible at once. We could count parts of some trees from a powerline tower several hundred meters uphill from them, and we also estimated numbers from that site after attempting to flush the colony to count them in the air. We explored the ground directly underneath the colony and also estimated size from there. Our estimate of 7,000–10,000 is probably conservative, as we were never able to view the entire colony at once.

Cultural and Resource Significance

Fruit bats play an important role in the ethnobiology of Samoa (Cox 1983). Samoans, though generally aware of the morphological and behavioral differences between *Pteropus samoensis* and *P. tonganus,* are often not aware that there are two different species. When we asked residents about the two color types, most replied that this was caused by a difference in age, sex, or possibly species. Knowledgeable residents know the two types of bats by different names. For *P. samoensis,* the common name we were given was "pe'a vao" (fruit bat of the forest); for *P. tonganus,* "pe'a fanua" (fruit bat of settled lands). For *P. samoensis,* Cox (1983) gave "pe'a vao", and for *P. tonganus,* "pe'a fai taulaga pe'a" (flying fox which makes flying fox towns). Whitmee (1875) listed "manu lagi" (animal of the heavens) as a local name for *P. samoensis,* after its habit of soaring high in the sky. There is a difference of opinion about the value of fruit bats in Samoa. Some Samoans consider fruit bats a unique and aesthetically valuable part of the environment; others see them as agricultural pests.

Fruit bats play an equivalent role in Fiji, where "beka" is the name applied to both species. An ancient Fijian fable asserts that fruit bats obtained their wings by stealing them from the rat, who as a consequence tries to eat young fruit bats at every opportunity; this explains why one frequently sees fruit bats carrying their young. Fruit bats are considered an important part of the environment by some Fijians, a food source by others, and an agricultural pest by some small farmers.

Hunting

Most hunting of bats in Samoa is for subsistence or commercial purposes, although Amerson et al. (1982) reported that some farmers shot bats to control agricultural damage. There also may be some shooting of bats for sport in American Samoa, according to some residents. Hunting pressure is much less in Fiji, where strict gun control regulations limit the take.

Subsistence Harvest

Fruit bats have long been used as a source of food in Samoa and Fiji (Whitmee 1875; Cox 1983). Whitmee wrote that during the breadfruit season many bats were killed for food, and Samoans even preferred bats over fowl. Whitmee (1875) reported, "At the present time they often shoot them: but the more common mode of catching them is to fasten a prickly bush on a long bamboo or light pole; with this they approach the tree on which a bat is feeding, and by a dexterous movement manage to strike a wing with a thorn of the bush as the animal takes to flight; the wing is thus torn by the thorns and the bat disabled."

Although still used as a source of food today, fruit bats are not sought for consumption as intensively in Samoa and Fiji as on certain other Pacific islands, such as the Marianas. While some Samoans and Fijians consider fruit bat to make a fine meal, others refuse to eat it. Use of fruit bats as food is more prevalent in Western Samoa than in American Samoa. Several hunters indicated to us that the Pacific Pigeon (*Ducula pacifica*) was the select quarry, and that fruit bats were taken incidental to pigeon hunting. The high cost of shotgun shells partly deters their liberal use on the less desirable bats.

In American Samoa, we observed subsistence hunters on several evenings in 1986. Hunters stationed themselves on a flyway or in agricultural forest where bats were coming to feed. Shotguns or .22-caliber rifles were used, and bats were shot on the wing or while roosting. *Pteropus tonganus* appeared to be the species commonly taken. Of

15 bats that we examined, 12 (80%) were *P. tonganus* and 3 (20%) were *P. samoensis*. *Pteropus samoensis* may be taken regularly by pigeon hunters during the day (Cox 1983). In 1989, we obtained an albinotic specimen of *P. samoensis*, shot earlier by hunters.

Commercial Harvest

Virtually all bats harvested for commercial purposes in Samoa have been exported to Guam or Saipan in the Marianas. To the best of our knowledge, such commercial harvest has been almost nonexistent on Fiji, although Wiles and Payne (1986) listed six imported into Guam in 1980.

An estimate of the number of bats shipped to Guam, where most are sent, is available from information collected by customs agents on Guam (Wiles and Payne 1986). The percentage of *P. samoensis* and *P. tonganus* in each shipment is not known, nor is the number of bats shipped to Saipan. Relatively small numbers of fruit bats entered Guam from American Samoa from 1980 to 1983, averaging 210 animals per year (Wiles and Payne 1986). In 1984, imports to Guam from American Samoa increased to about 1,630 bats. In 1985, about 1,000 were imported into Guam. Numbers dropped about 50% in 1986, and in November 1986, all commercial exports from American Samoa were banned. There have been no commercial shipments since then, although bats may be exported for personal use. No export permit has been required for bats shipped from American Samoa.

In American Samoa, commercial hunting of bats was more a sport than a lucrative business enterprise. Commercial hunting was generally done by small parties of hunters that pass shot along flyways at dusk. Because the vegetation is dense and the light usually poor, many bats were crippled and lost (W. Knowles, American Samoa Office of Marine and Wildlife Resources, personal communication; P. Cox, Brigham Young University, personal communication). Bats were frozen whole and stored until a sufficient number had accumulated for a shipment. We interviewed a local exporter who made five or six shipments in 1985, each with an average of about 200 bats (D. Spencer, personal communication). The exporter received $6.50 (U.S.) per pound for the bats from the Guam dealer. On Guam, bats were selling for about $14.00 per pound (G. Wiles, Guam Division of Aquatic and Wildlife Resources, personal communication). Bats with the white mantle (*P. tonganus*) made up the bulk of the harvest. After calculating the cost of shotgun shells and shipping, sale of bats was deemed to be only marginally profitable (D. Spencer, personal communication).

Commercial sale of fruit bats from Western Samoa began in 1981 (Wiles and Payne 1986). From 1981 to 1984, 18,750 were exported to Guam. During 1983 and 1984, Western Samoa was the most important supplier of bats to Guam, with about 8,350 and 6,650 imported in these 2 years. In 1985, about 7,000 bats were exported to Guam from Western Samoa and about 5,000 in 1986. Then, in the fall of 1986, exports from Western Samoa dropped significantly and remained low throughout 1987 and 1988. In 1988, 360 were imported into Guam from Western Samoa (G. Wiles, personal communication). This decline is believed to have resulted from one of the importers on Guam going out of business. For each shipment of bats from Western Samoa, a certificate of export is required from the Department of Agriculture. In 1987, both species of fruit bats found in Western Samoa were included on the Convention on International Trade in Endangered Species (CITES) Appendix II list, and in 1989, were upgraded to Appendix I. Thus, it is now illegal to commercially export bats from Western Samoa to Guam.

In Western Samoa, where wages are low, commercial hunting of fruit bats was viewed as a viable enterprise. There were evidently several major exporters who collected bats from a number of independent hunters. In the mid-1980's, one hunter on 'Upolu was given shotgun shells by an exporter and was paid (in Western Samoan) $3.00–4.00 (U.S. $1.50–2.00) for each bat (B. Emsley, American Samoa Office of Marine and Wildlife Resources, personal communication). Because shotgun shells are expensive and each bat represented a valuable commodity, there was probably less pass shooting and more hunting of roosting bats in Western Samoa than in American Samoa. Thus, it is probable that a lower percentage of bats were crippled and lost in Western Samoa.

Management Recommendations

Threats to Population

With the possible exception of the barn-owl (*Tyto alba*), which may take a few bats, there are few natural predators in Samoa. On Fiji, peregrine falcons may prey on bats, and smaller raptors such

as goshawks and harriers might possibly take young bats. The primary threat to both species of fruit bats in American Samoa, Western Samoa, and Fiji is the loss of habitat.

Hunting for local consumption has evidently never threatened either species in the past; it is the recent commercial exploitation of fruit bats that could excessively depress populations. The large numbers of bats shipped to the Marianas in the 1980's suggest that populations of both species have been subjected to increased hunting pressure, and several residents with whom we spoke indicated that bats were less common since the export trade became established. It is difficult to say how much of this decline is due to a reduction in bat numbers or to increasing secrecy of bats; the actual reduction in numbers cannot be determined without continuing systematic and comprehensive surveys. Commercial use of fruit bats is a threat that can be controlled, and was banned by local regulation in American Samoa in 1986. Western Samoa issued regulations in August 1989 directing the Comptroller of Customs to ensure and enforce the control of exportation of fruit bats and empowering the Chief Agricultural Quarantine Officer to search, seize, or refuse export of any fruit bats from any aircraft or vessel.

The loss of habitat due to logging and a growing human population will be more difficult to ameliorate. Timber is listed as the leading natural resource in Fiji, and lumber is listed as the fourth most important industry (Adams 1985a). Similarly, timber is listed as the only natural resource in Western Samoa; it is listed as the number four agricultural product, number one industry, and number four export (Adams 1985b). In Western Samoa, commercial logging has been an important source of revenue in recent years. Much of the interior of 'Upolu has been commercially logged and converted to pasture and other agricultural land. On Savai'i, logging is an even more important industry, although many of the logged areas are replanted or otherwise allowed to return to forest.

In American Samoa, commercial logging is not a viable industry, but in recent years much of the native forest has been removed and planted in taro and other crops. The loss of native forests and diverse agricultural forests will eventually limit the habitat available, especially for *Pteropus samoensis*. Conversion of native forest to diverse agricultural forests may not be detrimental to foraging habitat for *P. tonganus*, although a growing human population will probably increasingly disturb the remote areas where *P. tonganus* is currently able to roost.

On the positive side, viable populations of both species should be able to remain in both Fiji and Samoa; extinction for either species does not appear to be an imminent threat. The islands have a diversity of habitat types, often with rugged terrain. Much of this habitat is not easily accessed, making it difficult to eliminate fruit bats by hunting. About half of American Samoa remains in rain forest, ridge forest, and secondary forest, and much of this forest is too steep or otherwise unsuitable for development. Only about 20% of American Samoa is considered developable in the sense of having a slope of less than 30% (Amerson et al. 1982). On other islands in American Samoa, such as Ta'u, there has been minimal development, and formerly cultivated areas have returned to native forest. In Western Samoa, native forests cover about half of the land area; about one-third on steep terrain where their function must be protective rather than productive (M. Iakopo, personal communication). While conversion of native forest to pasture land or homogeneous coconut or cacao plantations may effectively eliminate habitat for fruit bats, conversion to diverse agricultural forest may not be so detrimental. Nonetheless, because little is known about fruit bat ecology and population dynamics, and because of the threats posed by the loss of habitat and commercial hunting, a conservative approach is recommended for fruit bat management in Samoa and Fiji.

Recommendations

There have been limited studies and surveys of fruit bats in Fiji and Samoa, and there are few data on which to base management decisions. Because of its naturally lower population density, *P. samoensis* is probably the more vulnerable of the two species. It may be possible to implement regulations that selectively protect *P. samoensis*. Our recommendations include the following:

1. Establish parks and reserves. With an expanding human population and an increasing demand for land, it is important that certain areas be established as parks or reserves. On Fiji, the Garrick Reserve and Colo-I-Suva Forest Reserve maintain important populations of both species of fruit bat. A large national park, O le

Pupu, has been set aside in Western Samoa on the south side of 'Upolu. This exemplary park preserves a tract of native forest that is inhabited by *P. samoensis*. Recently, a national park has been approved for American Samoa.

2. Protect colonies of *P. tonganus*. Hunting should not be allowed in fruit bat colonies, and the isolated mountain peaks, offshore islets, and craggy points that harbor colonies should be set aside as reserves. Major flyways should also be protected, if possible.
3. Prohibit hunting of fruit bats during the daytime. If the hunting of fruit bats was allowed only from sunset to sunrise, a larger percentage of the harvest would consist of *P. tonganus*, the more common of the two species. Also, *P. tonganus* colonies would be protected to some extent because most bats are away from colonies at night.
4. Establish a bag limit on fruit bats taken for subsistence. Any export of fruit bats for personal use should be limited to the daily bag limit. Special provision should be made for the taking of bats that are causing agricultural problems and for scientific research. Western Samoa recently added fruit bats to the list of "partially protected birds," thereby closing the hunting season from 1 April to 1 October each year.
5. Continue surveys and begin life history studies. This report represents preliminary information only, and many biological and ecological studies must be conducted before sound management practices can be implemented, including: marking or radio-tagging bats to determine home ranges, movement patterns, and population sizes; locating and visiting *P. tonganus* colonies to determine population size and social structure; analyzing food habits and foraging ecology; and questioning hunters about numbers harvested and other lore.
6. Map habitat types and vegetative communities. The amount of habitat available for fruit bats and other wildlife, and the rate at which it is being lost, is not well known, especially in Fiji and Western Samoa. Accurate vegetation mapping would provide this information.
7. Conduct a public education program. Regardless of the number of environmental regulations passed, enforcement of such laws will be difficult and only partially successful without an active public education program.

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Flying Foxes in the Solomon Islands

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Introduction

The Solomon Islands have a large bat population, and the most notable are the flying foxes. The relation of these remarkable creatures and their environment is not completely understood, but the life of the flying fox and the forest are inextricably linked.

Description of the Islands

The Solomon Islands are a widely scattered chain of mountainous islands and low-lying coral atolls stretching some 1,600 km in a southeasterly direction, from Bougainville in Papua New Guinea to the Santa Cruz Islands bordering the Republic of Vanuatu. The total land area is about 28,000 km^2. There are six major islands and hundreds of small ones. Most islands are rugged and forested.

The population of the Solomon Islands is about 300,000 people, with an annual growth rate of 3.5%. The density of the population ranges from 2.7/km^2 to 291.5/km^2 (these figures do not include urban areas). The large island of Isabel has a population density of 3.5/km^2, while the island of Malaita, a similar-sized island of 4,200 km^2, has 19.0/km^2. Some smaller islands have very high human population densities. The Reef Islands in the Temotu group have a population density of 176.5/km^2, and Tikopia in the same group has 291.5/km^2.

About 80% of the land is owned by families or tribes; the other 20% is controlled by government or privately owned. Solomon Islanders, about 85%, live in rural villages of up to 200 people. Because of the rugged nature of the terrain and the long sea distances between islands, many villages are isolated. Consequently, many of the people are involved in subsistence farming, others are engaged in mixed cash cropping. Most people grow up with and rely on the forest as the main source of raw materials. Subsistence farming (gardens), fishing, and hunting are the main sources of food. The principal exports are fish, timber, copra, palm oil, and cocoa.

Climate

The climate is tropical, and the islands are under the influence of the southeast trade winds. It is usually dry during April to November and wet November to April. The mean annual rainfall is between 300 and 500 cm in the lowlands. In some mountainous areas rainfall has been recorded in excess of 800 cm. The temperature is fairly constant, with a mean annual temperature of 28° C. Cyclones and associated storm activity are most likely to affect the islands between December and April. The last major cyclone was in 1986.

Vegetation

The flora of the Solomons is remarkably uniform from island to island, but poor in species composition when compared with other areas of tropical rainforest (Whitmore 1968). It appears that disturbance, probably because of cyclones, has been the main ecological factor determining floristic differentiation (Whitmore 1969).

The following vegetation types can be recognized (Hansell and Ward 1976): (1) lowland primary tropical rainforest—characterized by large-leaved, buttressed trees up to 45 m high, with tall woody climbers; (2) moss forest—trees 6–12 m high with smaller leaves than above and draped

with ferns, mosses, and hepatics; (3) areas of secondary growth—where primary forest has been cleared, the regrowth is often a tangle of low-level scrub and thicket; (4) open heath—with fern and bushes; (5) grass-covered areas; (6) saline swamp; and (7) freshwater swamp. The dominant vegetation type is lowland tropical rainforest, which runs into montane moss forest.

Flying Fox Management Issues

Status of Flying Foxes

There is little information available on the population status and the ecology of Solomon Islands flying foxes. While some information on distribution is available (Phillips 1968), most of the research to date has been on taxonomy, and much of this work is in need of revision.

There are 7 genera, 16 species, and 22 subspecies of Megachiroptera found in the Solomon Islands. Of these, one genus and at least 10 species are endemic. Further research in this area is likely to reveal new subspecies and possibly new species. The genus *Melonycteris* is currently under review (Flannery, unpublished manuscript).

Factors Affecting Flying Fox Populations

Habitat Change

The major factors contributing to habitat destruction and change in the Solomons are subsistence gardens, logging, and commercial agriculture. Shifting cultivation or subsistence gardens is often an environmentally sound type of resource use. However, there are areas where communities using this system are out of balance with their land resources. Population pressure and the customary land tenure system is adding to the rapid destruction of rainforest in some areas. Logging is being carried out on most large islands and some smaller ones; about 8,000–10,000 ha are logged annually.

Conflicts in Resource Use

Damage to tree crops by flying foxes was reported from several areas of the Solomons. Severe damage is reported on the Reef Islands, in the remote Temotu Province. No accurate information on the problem has been compiled. Lack of funding and staff have prevented any officers from the Environment and Conservation Division visiting the area to personally gather information.

The amount of conflict about resource use with flying foxes is not well known. Recent changes in the rainforests are expected to increase conflicts.

Subsistence Hunting and Commercial Harvesting

A conservation officer for the Solomon Islands said that during the late 1970's there was some commercial trade and export of flying foxes from the Solomon Islands (H. Isa, personal communication). Trading ceased when a group of hunters disappeared on a flying fox hunting expedition; all that was found was their canoe.

The flying fox is a source of protein for many people in the rural areas, although the degree of traditional harvesting is not well known. It seems the flying fox is not consumed in large quantities but is eaten only occasionally in most areas.

There is an increasing export trade in reptiles, amphibians, and insects from the Solomon Islands. There is also an export trade in crocodile (*Crocodylus porosus*) skin, turtle shell, mainly hawksbill (*Eretmochelys imbricata*), and coconut crabs (*Birgus latro*). Currently no legal export of flying foxes exists. Several companies have been interested in exporting flying foxes. Those who favor exporting argue that since some villagers kill flying foxes that cause damage to their tree crops, anyway, why not export them? This way villagers can make money and get rid of pests. Unfortunately, the solution is not that simple. Once the flying fox has a monetary value, bats would be killed not only for pest control but also to harvest, sell, and export. No program now effectively monitors export trade of flying foxes in the Solomon Islands.

Legislation

Little legislation is available that deals with wildlife. There are the Wild Birds Protection Act of 1914 and various Provincial by-laws for the management of some wildlife, but there is no national legislation for wildlife protection or management. By 1991 conservationists hope some basic wildlife protection legislation will be enacted.

Direction for Management

Like most Pacific Island nations, the Solomon Islands is changing at a rate that has put great pressure on traditional management systems. Large-scale exploitation of forest resources, min-

ing, commercial fishing, and export of wildlife has introduced a new set of criteria that cannot be readily absorbed into the traditional management systems in the Solomon Islands. Therefore, these new criteria are not usually subject to the checks and balances that have governed and guided people's actions for generations.

The challenge of the 1990's is to produce management systems, with traditional values, for the use of natural resources.

Future Research

There is an urgent need to collect information on the populations, status, ecology, and the habits of flying foxes from throughout the Solomons, particularly, from areas where there is resource conflict between farmers and bats, and where rapid habitat change is present. A clear understanding of the relation between the bat and its environment is necessary before commercial trade in flying fox species takes place.

A wealth of untapped traditional knowledge is available about many aspects of flying fox ecology. It is imperative this information be gathered before it is lost.

The Australian Museum, in conjunction with the Solomon Island Environment and Conservation Division, is presently conducting a national survey of the fauna of the Solomon Islands. The objective of the project is to gain a better understanding of the distribution, status, biology, taxonomy of faunal assemblages in relation to habitat, and conservation needs of Solomon Island fauna. The project will run for 1 year and will give a needed boost to the knowledge and understanding of the fauna of the Solomon Islands. Conservationists hope that more projects like this will be conducted in the near future.

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Current Status and Distribution of Fruit Bats (Genus *Pteropus*) in Papua New Guinea

by

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Introduction

Papua New Guinea is between the equator and latitude 12° S and between longitude 141° E and 164° E, and it has a total land area of 462,842 km^2. Politically, it is divided into 19 provinces and the National Capital District around Port Moresby. Papua New Guinea comprises the eastern half of New Guinea and includes the Bismarck Archipelago (principally New Britain, New Ireland, New Hanover, and Manus), the D'Entrescasteaux Islands, the Louisiade Archipelago, and the North Solomon Islands of Bouganville and Buka.

In a country where 97% of the land is held under customary tenure, development of conventional national parks and reserves has proven difficult. In Papua New Guinea, conservation areas currently cover 2.3% (10,656 km^2) of the land area. Wildlife management areas cover 10,529 km^2, while National Parks cover only 127 km^2 (Asigau 1989). Wildlife management areas, an attempt to develop conservation on a customary basis using traditional methods of resource management, are more acceptable than National Parks to promote protected areas in Papua New Guinea.

The need for more conservation areas for protection of biodiversity is a priority. To successfully devise programs a data base was established by the department and is an ongoing project. The records are kept manually to provide information on the distribution of bird and mammal species so that an assessment of their rarity can be made. These data are used to determine which species may require more detailed study as potentially rare or threatened species and to provide information on areas where the composition of the fauna is unknown. Currently the process is very slow and requires financial assistance to upgrade the facilities. The information I provide here is the result of data collection by department staff over a number of years.

Laurie and Hill (1954) recognized 23 species of *Pteropus* containing 49 subspecies in the area, but the genus appears to need complete revision.

Twelve species have been recorded in Papua New Guinea: *Pteropus admiralitatum, P. alecto, P. conspicillatus, P. gilliardi, P. hypomelanus, P. macrotis, P. mahaganus, P. neohibernicus, P. rayneri, P. scapulatus, P. temmincki,* and *P. tonganus.* I discuss only nine of these species for which there is some knowledge (see Appendix) of their distribution and status: *Pteropus admiralitatum, P. alecto, P. conspicillatus, P. hypomelanus, P. macrotis, P. neohibernicus, P. rayneri, P. temmincki,* and *P. tonganus.*

Administration and Legislation

There is no specific environmental legislation directed primarily towards the conservation of flying foxes in Papua New Guinea. Protection is afforded, however, under a number of acts administered by the Department of Environment and Conservation.

The following acts deal directly with the establishment of protected areas: Fauna (Protection and

Control) Act, National Parks Act, and Conservation Areas Act. Under the National Parks Act, the Assistant Secretary of the National Parks Branch is responsible for the administration and management of national parks, provincial parks, historical sites, nature reserves, national tracts, and other protected areas. Wildlife management areas, which are declared by the Minister for Environment and Conservation under the Fauna (Protection and Control) Act, are managed by the landowners themselves, who are also responsible for making the rules (Kwapena 1984; Asigau 1989).

The following legislation administered by the department is important for protection of habitats and organisms.

Fauna (Protection and Control) Act of 1978

Significant aspects of this act include the establishment of wildlife management areas within which major wildlife species (e.g., birds of paradise, cassowaries, crocodiles, wallabies) may be used under a suitable management and cropping program for the benefit of the resource owners. Sanctuaries also are provided within these areas. A management committee including representatives of the resource owners manages each wildlife management area.

The act also establishes a list of protected species that may not be hunted or held in captivity without permission of the Conservator of Fauna. The conservator, in cooperation with Customs Division, also controls the export and import of wildlife.

National Parks Act of 1982

This act provides for the investigation, negotiation, and purchase and lease of land for the establishment of national parks and other similar reserves that will constitute a park system in Papua New Guinea.

Conservation Areas Act of 1978

This act provides for the protection of certain sites, lands, and landforms that may be considered important for conservation and which form part of the national heritage of Papua New Guinea. The establishment of a management committee for each area ensures that the customary land tenure system covering land and resource ownership is fully considered.

Customs Regulations Act of 1979

Before any animals or parts of animals, alive or dead, can be exported or imported from Papua New Guinea, a permit must be issued by the Conservator of Fauna; the Secretary of Department of Environment and Conservation is appointed for this responsibility.

International Trade (Fauna and Flora) Act of 1979

Through this act, Papua New Guinea has implemented the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) by fully controlling the import and export of protected species of fauna and flora between member countries.

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Appendix

Scientific name: *Pteropus alecto* Temminck, 1937
Common name: Black flying fox
Synonyms: *Pteropus gouldii* Peters, 1867
Pteropus morio Anderson, 1908
(?)*Pteropus nicobariious* Heude, 1896
Extralimital distribution: Coastal northern Australia north of 5°; Celebes Sumba, Lombok; Savu, Saleyer Islands; and Irian Jaya, Indonesia
Roosting sites: In mangroves, paperbarks (*Melaleuca*), and occasionally patches of rainforest. Reported from cave in northern Australia.
Description: Head, back, rump, and entire underside blackish or blackish seal-brown thinly sprinkled with whitish or buffy hairs; mantle dark chocolate brown not differing markedly from rest of back. Region around eyes washed with dark brown. Color is glossy on back and rump but dull on under surface.
Pteropus gouldii is rare (Flannery 1989) and has a restricted range in Papua New Guinea. Little is known about the species. Known localities include Bugi and Morehead in Western Province, and Yule Island in Central Province.

Scientific name: *Pteropus macrotis* Peters, 1867
Common name: Big-eared flying fox
Synonyms: *Pteropus insignis* Rosenbery, 1867
Pteropus (*Epomops* ?) *epularius* Ramsay, 1878
Extralimital distribution: Aru Island, Irian Jaya
Roosting sites: Unknown
Description: Head dark brown passing to cream-buff to an orange ochraceous-buff on back of head and mantle. Back and rump dark brown. Underside from chin to anus, including flanks, glossy dark brown to blackish. Fur short. Ears long and pointed (33–36 mm).
This species was recorded at various localities in Papua New Guinea from the Western Province in the west to Milne Bay Province in the east. In Western Province, it was recorded in Tonda Wildlife Management Area. It has also been recorded in East Sepik Province. It is probably widespread throughout most of the lowlands.

Scientific name: *Pteropus temmincki*, Peter 1867
Common name: No local common name
Synonyms: *Pteropus capistratus* Peters, 1876
Pteropus petersi Matschie, 1899
Pteropus liops Thomas, 1910
Extralimital distribution: Amboina, Ceram, Timor, Buru Island, Indonesia
Roosting sites: Unknown
Description: Head cream buff or cream white with three longitudinal dark brown stripes on face—one between the eyes and one on either side below each eye. Mantle golden buffy shading to creamy white posteriorly. Back and rump silvery buff-white or cream-buff typed hairs over dark-brown base. Breast, belly, and flanks similar to upper surface but pale hair tips generally strongly contrasting with the pale tips of the hair, which gives the animal its overall pale appearance. Uncommon spe-

cies, confined to Bismarck Archipelago (New Ireland, Duke of York Island, and New Britain).

Scientific name: *Pteropus neohibernicus* Peters, 1876
Common name: Greater flying fox
Synonyms: *Pteropus melanopagon* var. *neohibernicus* Peters, 1876
Pteropus degener Peters, 1876
Pteropus rufus Ramsay, 1871
Pteropus melanopagon var. *Papuana* Peters and Doria, 1881
Pteropus sepikensis Sanbourn, 1931
Pteropus neohibernicus hilli Felten, 1961
Extralimital distribution: Irian Jaya, Miscool, and Ghebi Islands
Roosting sites: Unknown
Description: Color is variable, but the fur of the back is sparse or almost absent. *Pteropus neohibernicus*, the largest of our flying foxes, is a common and widespread species found throughout most of the country below 1,000 m. This species can survive on small islands, as demonstrated by its presence on Karkar Island, Madang Province, Papua New Guinea. Why it does not spread to other larger islands (D'Entrecasteaux and Louisiade Archipelago) remains a mystery.

Scientific name: *Pteropus conspicillatus* Gould, 1850
Common name: Spectacled flying fox
Synonyms: *Pteropus chrysauchen* Peters, 1862
Pteropus mysolensis Gray, 1870
Extralimital distribution: Halmahera Group and islands between them and Irian Jaya, Australia
Roosting sites: Mangroves, tall trees in swamps and rainforest
Description: Face and crown of head black with distinct ring of pale brownish yellow around each eye, extending slightly forward on each cheek. Back of head, neck, and shoulders pale straw yellow; chin, throat, breast, and abdomen black with few scattered yellowish or whitish hairs; back similar, contrasting strongly with pale yellowish mantle. Easily confused with *Pteropus alecto,* from which it is distinguished by its brighter, contrasting mantle and clearly defined rings around the eyes. This species is uncommon and almost nothing is known about the biology of our population (Flannery 1989). *Pteropus conspicillatus* is found on Woodlark, Kiriwine Island, southeast of Papua New Guinea. Recorded sightings on the mainland are scattered, at sea level along the northwest and southeast of the mainland.

Scientific name: *Pteropus rayneri* Grey, 1870
Common name: No local common name
Synonyms: *Pteropus grandis* Thomas, 1887
Pteropus rubianus Anderson, 1908
Pteropus lavellanus Anderson, 1908
Pteropus cognatus Anderson, 1908
Pteropus rayneri moncensis Lawrence, 1945
Pteropus rennelli Trougthon, 1929
Extralimital distribution: Solomon Islands
Roosting sites: Forest trees, mangroves, coconut palms
Description: (Of *Pteropus rayneri grandis*) Head blackish. Mantle and back of neck dark chocolate to dark reddish brown, black glossy blackish to seal-brown. Rump from pale yellowish white to ochraceous buff, contrast-

ing strongly with dark brown of back and mantle. Center of breast and upper belly blackish, forming a large patch or a broad stripe. Rest of breast, chest, belly, and flanks dark chocolate. Overall appearance is of dark brown to blackish animal with pale rump.
Subspecies *Pteropus rayneri grandis* was recorded from Bouganville and Buka Island in Papua New Guinea. It is widespread and is common on these islands.

Scientific name: *Pteropus tonganus* Quoy and Guimard, 1830
Common name: No local common name
Synonyms: *Pteropus tonganus* Quoy and Gaimard, 1830
Pteropus geddiei MacGillivary, 1860
Pteropus basilicus Thomas, 1915
Pteropus vanikorensis
Extralimital distribution: Solomon Islands, New Caledonia, Fiji Islands, Cook Island
Roosting sites: Unknown
Description: Head dark brown to blackish; chin and throat blackish or seal brown. Mantle and back of head from cream buff to pale ochraceous-buff. Back, rump, breast, belly, and flanks blackish or seal brown, thinly sprinkled with white; dark- headed individuals often have pale russet or buffy russet suffusion around the eyes giving a "spectacled" appearance similar to *Pteropus conspicillatus*.
The status of this species is unknown, but the subspecies *Pteropus tonganus basilicus* was recorded by Thomas on Karkar Island in Papua New Guinea (Laurie and Hill 1954). Little information exists on this species.

Scientific name: *Pteropus hypomelanus* Temminck, 1853
Common name: Variable flying fox
Synonyms: *Pteropus condorensis* Peters, 1869
Pteropus tricolor Gray, 1870
Pteropus macassarious Heude, 1896
Pteropus geminorum Miller, 1903
Pteropus enganus Miller, 1906
Pteropus hypomelanus canus Anderson, 1908
Pteropus lepidue Miller, 1900
Pteropus hypomelanus annectens Anderson, 1908
Pteropus hypomelanus tomesi Peters, 1868
Pteropus cagaryanus Mearns, 1908
Pteropus hypomelanus luteus Anderson, 1908
Extralimital distribution: Thailand, Vietnam, and adjacent islands, through Indonesia to Solomon Islands
Roosting sites: Trees
Description: Head dark brown. In some specimens the dark brown is restricted to the muzzle region and progressively lightens to a light brown to yellowish brown near the ears. Mantle pale yellowish. Back and rump dark brown to reddish brown. Breast and belly from golden ochraceous buff to cream buff. In most specimens this color extends uniformly over the entire breast and belly, but in some specimens the hind part of the belly passes into a dark brown similar to the back. Flanks brownish, similar to back.
This rare species (Flannery 1989) has been recorded widely on islands southeast of the mainland: Kiriwina Island, Trobriand Island, and Lou-

isiade Archipelago. It also has been recorded on Karkar Island northeast of Papua New Guinea.

Scientific name: *Pteropus admiralitatum* Thomas, 1894
Common name: No local common name
Synonyms: *Pteropus solomonsis* Thomas, 1904
Pteropus colonus Anderson, 1908
Pteropus goweri Tate, 1934
Extralimital distribution: Solomon Islands
Roosting sites: Unknown
Description: Fur long; crown and face pale grey; back of neck and shoulders cinnamon brown; back dark brown mixed with white hairs; chin throat, abdomen, and sides of body uniform dark brown, thickly mixed with silvery white or yellowish hairs. Size small (for *Pteropus*), forearm 108–126 mm, ears short (17–20 mm) and not protruding from hair on head by great amount; most similar to *Pteropus mahaganus* from which it is distinguished by smaller size and suffusion of white throughout fur, and *Pteropus hypomelanus* from which it is also distinguished by its smaller size, and *Pteropus hypomelanus* from which it is distinguished by always having the center of the abdomen lighter in color than the sides of the body.

This common species is confined to Manus Province, Admiralty Island, Papua New Guinea. Locally, it is used for food by the people. Recent logging proposed for the area will definitely affect the roosting sites.

Distribution of Pacific Island Flying Foxes

by

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Introduction

The geographic range of flying foxes (Megachiroptera: Pteropodidae) comprises much of the tropics and subtropics of Africa, Asia, and Oceania (Fig. 1). Within this region, lack of food excludes them from extremely arid areas such as central Australia, northwestern Africa, and most of the Arabian peninsula. Their diet consists almost entirely of plant reproductive parts (fleshy fruits, flowers, nectar, and pollen), to a lesser extent leaves, and sometimes water (Marshall 1983, 1985). In arid or semi-arid regions, such as southern Iran or Pakistan, they survive by foraging in local areas of higher plant productivity, such as forest islands along seacoasts and watercourses or on tree crops in isolated oases (Roberts 1977; DeBlase 1980). In well vegetated, but seasonally dry habitats, such as parts of Africa and Australia, flying foxes may migrate several hundred kilometers to follow seasonal patterns of fruiting or flowering (Nelson 1965; Marshall 1983).

The current northern limit of flying fox distribution in Asia seems set by inland aridity in the west and quite dramatically north of India by the mountain wall of the Himalayan uplift. In southeast Asia, where physical barriers are less overt, the factors limiting northward range expansion are unclear. Presumably in eastern Asia, along most of the Mediterranean coast, and in the Tasman Strait, increasing seasonal restriction of fruit production (Wallin 1969; Howe 1986) and decreasing average and minimum winter temperatures at higher latitudes set range limits.

Most of the region that was the focus of this conference (the Pacific islands, including the Philippines and Papua New Guinea, but excluding Australia, Indonesia, and the islands of the Asian continental shelf) has a humid tropical climate with very limited to moderate seasonal variation in temperature, day length, and rainfall. The factors which set the current eastern limit of the range of flying foxes in this region are also unclear. North of the equator the range limit is reached on Kosrae, Federated States of Micronesia (FSM), the easternmost high island in Micronesia. Flying foxes are seemingly absent from the atolls of the Marshall Islands, as well as Kiribati, Tuvalu, Nauru, and Tokelau to the southeast. Yet high flying fox densities on Ulithi Atoll, FSM (Wiles et al. 1991), for example, illustrate that they can persist on small, isolated atolls where habitats have a long history of human alteration for tree crop production. South of the equator, flying foxes occur considerably farther east, reaching the high islands of Mangaia and Rarotonga in the southern Cook Islands (Wodzicki and Felten 1980). However, they are not reported from the rest of the Cook Islands, nor the high islands and atolls of French Polynesia still farther east. Archaeological investigations offer no indication that flying foxes were formerly present in these areas (D. W. Steadman, personal communication).

Distribution of Microchiroptera and Megachiroptera

Microchiropteran bat species outnumber the Megachiroptera (776 species versus 174 species; Hill and Smith 1984). In the Old World, there is only one extant microchiropteran species reported to consume significant amounts of fruit and nectar—*Mystacina tuberculata* in New Zealand (Daniel 1976). Virtually all other Old World microchi-

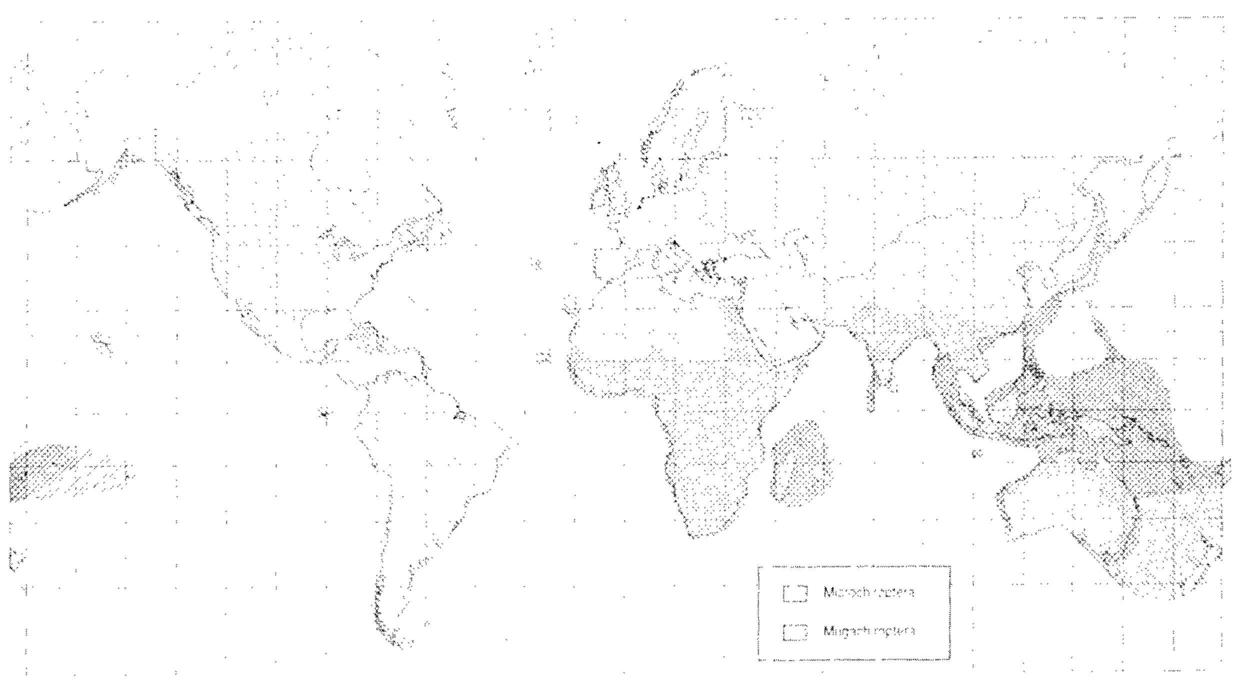

Fig. 1. Global distribution of Megachiroptera and Microchiroptera (Hill and Smith 1984; Koopman, personal communication).

ropterans feed exclusively on insects and other arthropods, though a few, predominantly tropical, species eat small vertebrates. The composite range of microchiropterans overlaps broadly with that of flying foxes and extends beyond it (Fig. 1), both farther into the arid areas mentioned earlier, to islands in the Atlantic and Pacific oceans, and much farther toward the North and South poles (Koopman 1970; Hill and Smith 1984). However, microchiropterans seemingly are absent from islands at or near the eastern edge of flying fox distribution in the Pacific (Kosrae, Niue, Mangaia, and Rarotonga) and on Rodrigues, in the western Indian Ocean (Cheke and Dahl 1981).

The Pattern of Flying Fox Species Diversity

In considering the ranges of genera, species, and subspecies, it is important to be aware that the number of flying fox species recognized by taxonomists changes over time, and that the geographic range of many taxa is very poorly known. The number of taxa increases both from field collections of animals which are immediately evident as unknown to science (e.g., *Pteralopex acrodonta*, a distinctive Fijian flying fox described by Hill and Beckon 1978), but more frequently from the systematic analysis of museum specimens accumulated over time, which reveals distinctions earlier investigators with more limited samples failed to detect. The latter process can also lead to the elimination of taxa when errors are discovered, apparent differences among taxa vanish with larger sample sizes, or taxonomic methods and philosophies change. This means that the numbers given here for species in a genus or in a country are part of a progress report and are approximate. Slightly differing assessments of the number of species in the genus *Pteropus* or of flying fox genera do not affect the general patterns and interpretations emphasized in this review.

Figure 2 shows estimated numbers of flying fox species by country. In some regions (e.g., Southeast Asia) numbers were extrapolated from adjacent countries with better records. It is immediately apparent that the highest diversity occurs in Indonesia, which cuts across several major zoogeographic regions with at least partially distinct faunas (Koopman 1989). Adjacent areas show relatively high within-country diversity, but isolated, smaller islands of both the Pacific and Indian oceans typically have fewer than five species.

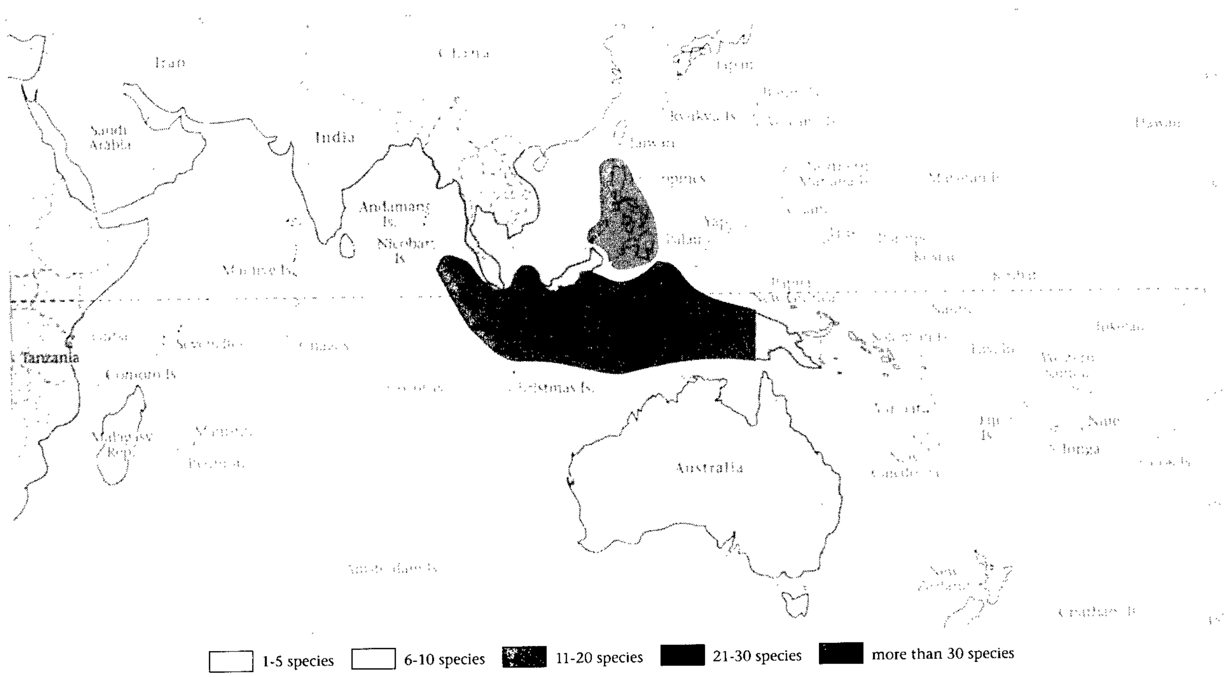

Fig. 2. Flying fox species density distribution by country in the IndoPacific region (Kingdon 1974; Lekagul and McNeely 1977; Roberts 1977; Koopman 1979, 1982, 1989, 1992, personal communication; DeBlase 1980; Honacki et al. 1982; Heaney et al. 1987; Nowak and Paradiso 1983).

A few of these small island taxa are wide-ranging species; most are local endemics.

As knowledge of Pacific island faunas increases, species numbers in the already more diverse areas will likely show the greatest increases. To the extent that biological surveys precede extensive habitat alteration and widespread availability of guns, the larger, higher islands of the southwestern Pacific, particularly in montane areas, offer the greatest prospect of finding previously unknown flying foxes. The limited vertebrate faunas of many of the more isolated, smaller islands, for example, in eastern Polynesia or the Mascarenes, are better known.

Distribution of *Pteropus* and *Acerodon*

Because a primary focus for this conference was the commercial trade in flying foxes to the Marianas, the remainder of this discussion will emphasize the two genera of large flying foxes — *Pteropus* and *Acerodon* — which have appeared in trade and are now listed on Appendix II of Convention on Trade in Endangered Flora and Fauna (CITES).

Distribution of Pteropus

With more than 50 species, *Pteropus* is by far the most diverse flying fox genus. Its wide range extends from Madagascar and some Indian Ocean islands in the west, across the southern margin of Asia, through much of the Pacific from the Ryukyu and Bonin islands in the north, to southeast Australia, and New Caledonia in the south, and east to the Cook Islands (Fig. 3). Its primary distribution is in the Pacific, with 46 of the 56 species occurring east of the Indian Ocean.

One feature of the distribution of *Pteropus* has puzzled biologists since it was first detected. *Pteropus* species occur on the islands of Pemba and Mafia, a few tens of kilometers off the east coast of Tanzania. Though other *Pteropus* species might move similar distances foraging in one night, there is no evidence that either species is established on the African mainland. Kingdon (1974) reviewed the various explanations, but concluded that none was well supported.

Pteropus is primarily an island taxon, with 48 species (86%) found only on islands. Only eight species occur on major continental land masses (four in Asia and four in Australia), and most of these have a primarily coastal distribution. The

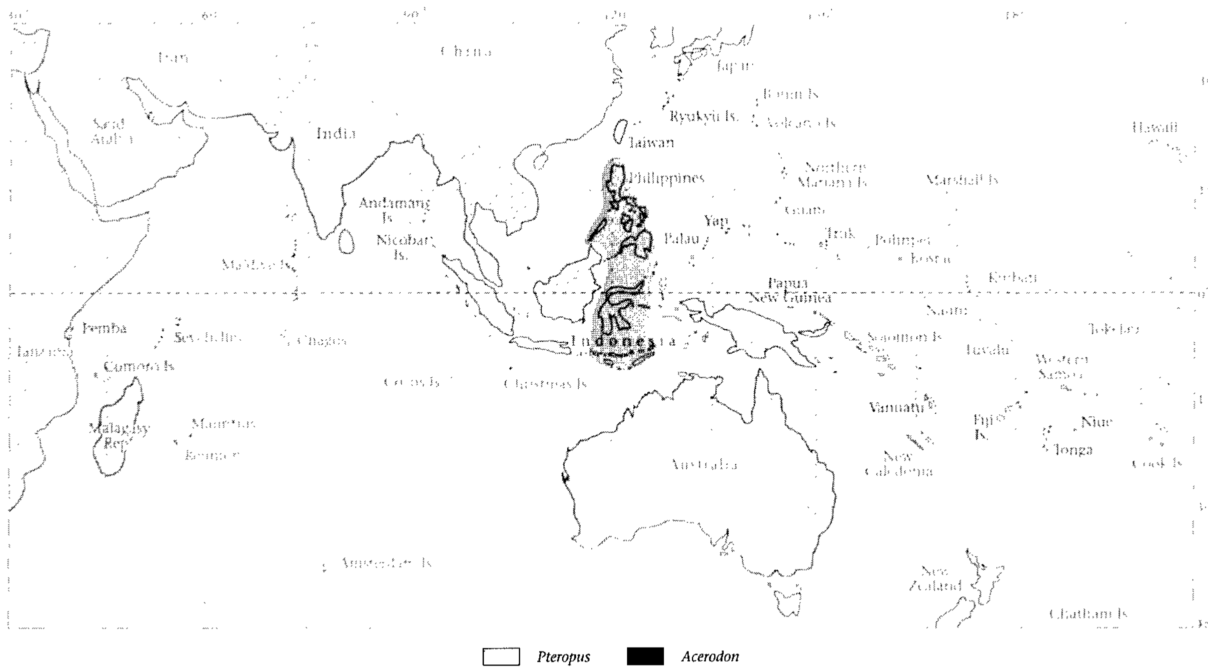

Fig. 3. Distribution of *Pteropus* and *Acerodon* (Musser et al. 1982).

majority of species have limited or very limited distributions (Table), with 38 species (68%) confined to land areas of <50,000 km². Half (23) of all the species have ranges <10,000 km²; 15 (27%) <1,000 km². Only five (9%) have ranges greater than 1 million km². Although surveys in less-well-studied regions would result in range extensions for some species, it is more likely that the ranges given in the Table are overestimates for many species. Where recent distribution maps are available—for the Australian species (Strahan 1983)—reasonably accurate range area estimates can be

Table. *Land area (km²) of known ranges for* Pteropus *species (based on Honacki et al. 1982 and Koopman, submitted). Species listed on Appendix I of CITES are in boldface.*

Very limited	Limited		Moderately broad		Broad	
<1,000	1,000–9,999	10,000–49,999	50,000–99,999	100,000–499,999	500,000–999,999	>1,000,000
argentatus	*dasymallus*	*admiralitatum*	*personatus*	*caniceps*	*neohibernicus*	*alecto*
brunneus	*faunulus*	*anetianus*	*speciosus*	*conspicillatus*	*rufus*	*giganteus*
fundatus	*livingstonei*	*chrysoproctos*	*temmincki*	*griseus*		*poliocephalus*
howensis	***mariannus***	*gilliardi*	***tonganus***	*hypomelanus*		*scapulatus*
insularis	*niger*	*lombocensis*		*leucopterus*		*vampyrus*
molossinus	*pohlei*	*mahaganus*		*lylei*		
nitendiensis	*seychellensis*	*melanotus*		*macrotis*		
phaeocephalus	*subniger*	*melanopogon*				
pilosus		*ocularis*				
pselaphon		*ornatus*				
rodricensis		*pumilus*				
sanctacrucis		*rayneri*				
tokudae		***samoensis***				
tuberculatus		*vetulus*				
voeltzkowi		*woodfordi*				

calculated, but for species with few distributional data, the area estimates are approximate. Generally, even for species known from only one or two localities (e.g., *P. gilliardi* in New Britain, *P. pilosus* in Palau, and *P. caniceps* in Sulawesi), the total land area of an island or island group was used. Yet, flying fox species, particularly on larger islands, such as New Guinea and New Caledonia, typically occur only in a subset of the available habitats (e.g., lowland rainforest, but not high elevation cloud forest, or vice versa).

Distribution of *Pteropus* Species on CITES Appendix I

The ranges of the seven Pacific island species currently listed on Appendix I of CITES (Fig. 4) are discussed below by subspecies. With the exception of *P. tonganus,* all have either limited or very limited distributions (Table).

Pteropus mariannus occurs north of the equator in portions of Micronesia and, at least formerly, in the Ryukyu Islands, south of Japan. This species closely resembles (and is considered taxonomically allied to) *P. tonganus,* which is found only south of the equator (Andersen 1912).

Pteropus m. loochoensis was described from two nineteenth century specimens from Okinawa (1,176 km^2 total range), Ryukyu Islands (Andersen 1912). Yoshiyuki (1989) re-examined these specimens and regards *P. loochoensis* as a species distinct from *P. mariannus*. Recent collections and field work on flying foxes in the Ryukyus have offered no evidence that this taxon still exists (H. Ohta, personal communication). The lack of additional, independently collected, Okinawan specimens leaves some uncertainty as to whether the type specimens actually were collected there.

Pteropus m. mariannus is confined to the islands of Guam, a U.S. Territory, and Aguijan, Rota, Tinian, and Saipan, all within the Commonwealth of the Northern Mariana Islands (CNMI; 872 km^2). Aspects of the status and management history of this subspecies are treated by several authors in this volume.

Pteropus m. paganensis occurs on Pagan (48 km^2) and Alamagan (11 km^2) in the CNMI. *Pteropus mariannus* populations on the other northerly islands in the CNMI have not been assigned to a subspecies (Wiles and Glass 1990). Wiles and Glass (1990) also noted that original description of *P. m. paganensis* is based on a small sample, and evidence of interisland movement calls into question the presence of two subspecies in the Marianas Islands. Wiles et al. (1989) offered recent flying fox population estimates for this region.

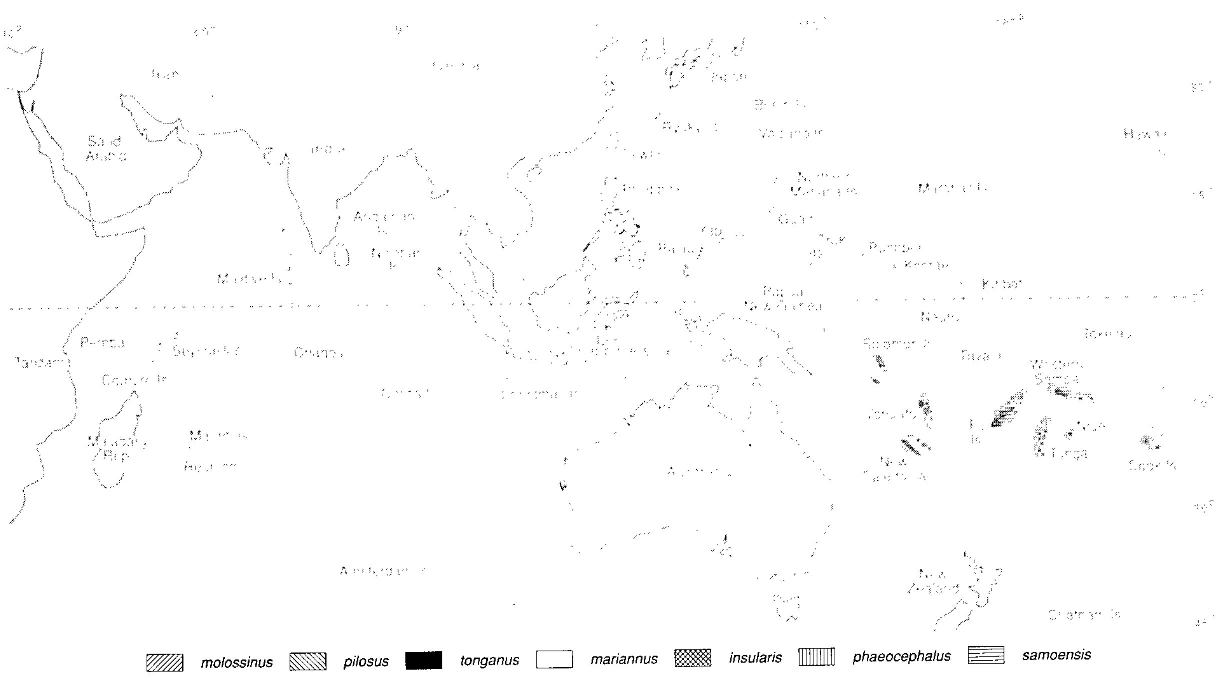

Fig. 4. Distributions of *Pteropus* species currently listed on Appendix I of CITES.

Pteropus m. pelewensis is limited to Palau, a U.S. Trust Territory in the western Caroline Islands (464 km^2; Andersen 1912; Perez 1968). Wiles and Conry (1990) reported on flying fox numbers observed in a Palau nature reserve. Flying foxes, presumably *P. mariannus*, are reported from Sonsorol and Fanna, two of the outlying islands of the far southwest Carolines, which are politically part of Palau (Engbring 1983).

Pteropus m. ualanus occurs only on Kosrae, FSM (110 km^2; Andersen 1912). This subspecies defines the eastern limit of the range of *Pteropus* north of the equator and is separated from the rest of the range of *P. mariannus* (more than 2,000 km from the nearest known population of this species).

Pteropus m. ulthiensis is confined to Ulithi Atoll, FSM (4.5 km^2), 161 km northeast of Yap. This population was recently censused by Wiles et al. (1991). They noted that bats, which may be allied to *P. mariannus*, are reported by residents of some other isolated islands and atolls in eastern Yap state.

Pteropus m. yapensis is found only on the Yap Islands, FSM, with a total land area of 99 km^2. Falanruw (1988) offered extensive information on this subspecies, noting that the body size differences reported as distinguishing it from *P. m. pelewensis* were not reliable.

Pteropus tonganus, with three recognized subspecies, is the most widely distributed of the listed species, occurring on scattered islands from the north coast of New Guinea to the Cook Islands in eastern Polynesia. Koopman (1979) characterized it as a supertramp species, occurring primarily on smaller, often more isolated, islands with low bat diversity, but absent from large, species-rich islands in the same region.

Pteropus t. basiliscus is generally viewed as restricted to the vicinity of Karkar Island, Papua New Guinea (368 km^2; Koopman 1979). A *P. tonganus* specimen in the British Museum from the Schouten Islands some 200 km west, off the mouth of the Sepik River, is presumably allied to this subspecies.

Pteropus t. geddiei occurs in the the Solomon Islands, Vanuatu, and New Caledonia (including the Loyalty Islands)—a total land area of 38,315 km^2. In the Solomons, it was recorded only from Rennell Island and the Santa Cruz Islands (Hill 1956; Phillips 1968), until it was recently found on Malaita (Flannery 1989). Flannery (personal communication) believes that it may be widespread, but uncommon throughout the archipelago. In Vanuatu, it is widespread and common (Chambers and Esrom 1988), while in New Caledonia it was uncommon (Sanborn and Nicholson 1950).

Pteropus t. tonganus extends from Fiji, Tonga, Wallis, Futuna and Samoa to Niue, and the southern Cook Islands of Rarotonga and Mangaia, covering a total land area of approximately 22,557 km^2 (Andersen 1912; Wodzicki and Felten 1975, 1980; Hill 1979). The Cook Islands populations (which are the smallest in a size cline across the range of this subspecies) define the eastern limit of flying fox distribution in the Pacific (Wodzicki and Felten 1980).

Pteropus molossinus, with no subspecies, is known from Pohnpei and the adjacent small atolls of Ant and Pakin, FSM, which total approximately 330 km^2 (Andersen 1912; Jackson 1962; Johnson 1962; Bruner and Pratt 1979; personal observations). We believe that the sole record of this species from the Mortlock Islands, FSM (Andersen 1912), is likely a locality error, and that the species is limited to the above localities.

Pteropus samoensis of Fiji and Samoa has two extant subspecies (Wodzicki and Felten 1975).

Pteropus s. nawaiensis is found in Fiji (18,330 km^2). The details of its distribution in Fiji are not fully known, but records are available for several islands, both large and small (Sanborn 1931; Pernetta and Watling 1978; K. Koopman, personal communication).

Pteropus s. samoensis occurs in Western Samoa (2,840 km^2) and the U.S. Territory of American Samoa (190 km^2). It is reported from or likely to occur on all the major islands and nearby forested islets, but not on isolated Swains and Rose atolls, which are politically part of American Samoa.

Pteropus insularis is known from the islands of Chuuk (formerly Truk) Lagoon (117 km^2), FSM (Andersen 1912; Bruner and Pratt 1979; G. Wiles, personal communication). Though the lagoon is some 65 km across at its widest point, distances among islands are not large. Bats occur on and presumably move among all of the forested islands, including cays on the barrier reef margin (personal observation). Specimens in the British Museum indicate an isolated population allied to *P. insularis* occurs on Namonuito Atoll (4.4 km^2), 180 km northwest of Chuuk Lagoon.

Pteropus phaeocephalus is found only on the Mortlock Islands, FSM (less than 12 km^2), a series of islands and atolls extending more than 300 km southeast from Chuuk Lagoon (Andersen 1912).

Details of distribution across this group of atolls and islands are not known, but recent reports of bats (not identified to species) are available for Namoluk (Marshall 1975), Losap and Satawan (M. Henry and C. Glover, personal communication). As one of apparently several distinct, but related, populations on isolated atolls in Chuuk State, this species may eventually be considered a subspecies of *P. insularis* (K. Koopman, personal communication).

Pteropus pilosus is based on two specimens collected in Palau (464 km²) before 1900 (Andersen 1912; K. Koopman, personal communication). The species is quite distinct from *P. m. pelewensis*, and no additional specimens have been detected in examinations of multiple flying fox trade shipments from Palau to Guam (Wiles and Payne 1986; G. Wiles, personal communication) nor in field surveys in Palau (Wiles and Conry 1990; G. Wiles personal communication). It thus seems to be extinct in Palau proper. Since, as noted earlier, flying foxes are reported from two isolated islands of the southwestern Carolines (Engbring 1983), a small possibility exists that the species persists there.

Distribution of Acerodon

Acerodon is closely related to *Pteropus* and is distinguished only by dental features (Musser et al. 1982). The range of all currently recognized species of *Acerodon* occupies a limited area near the center of the range of *Pteropus* (Fig. 3). The following species distribution data rely largely on Musser et al. (1982).

Acerodon celebensis occurs on Sulawesi, Indonesia, and smaller adjacent islands (known from Sula Mangole, Salayar, and Siao; Bergmans and Rozendaal 1988), which total approximately 191,561 km². Bergmans and Rozendaal (1988) reported numbers of live *A. celebensis* regularly for sale in Manodo, northern Sulawesi.

Acerodon humilis occurs only in the Talaud Island, Indonesia (1,282 km²), which form stepping stones between the southern Philippines and Sulawesi.

Acerodon jubatus is found throughout the Philippines, except Palawan and the adjacent Calamianes Islands, an area of 286,621 km². Heaney et al. (1987) judge it to be widespread, but declining.

Acerodon lucifer is known only from specimens collected on Panay, Philippine Islands (11,519 km²) in the last century. The species is thought to be extinct (Heaney et al. 1987).

Acerodon leucotis is known from Balabac, Palawan, Busuanga, and Philippine Islands (12,740 km²). Heaney et al. (1987) suggested it may be common in forest areas.

Acerodon mackloti is the southernmost *Acerodon* species recorded from several of the Lesser Sunda Island (Lombok, Sumbawa, Flores, Alor, Sumba, and Timor; 82,608 km²). On Lombok, Goodwin (1979) observed that the species was hunted, but two colonies of several hundred bats remained adjacent to villages.

Distribution and Conservation

Limited Total Range

Species or subspecies of flying foxes with very small total ranges are clearly more vulnerable to human intervention (hunting, habitat alteration, and introduction of predators) and locally intense natural hazards (typhoons, epidemics, and volcanism) than wide-ranging taxa. What may be less evident is that human intervention and natural hazards interact synergistically in a variety of ways to increase extinction risks. For example, extensive forest clearance both concentrates bats in remaining forest fragments and increases the vulnerability of remaining trees to windthrow in storms. Elsewhere in this volume, factors affecting flying fox survival are treated both in general terms and discussed for specific islands. Not surprisingly, all three of the *Pteropus* species which have become extinct since 1800 (*P. subniger*, *P. pilosus*, and *P. tokudae*) have total ranges less than 10,000 km². Of the surviving 20 species with similar range areas (Table), some recent data are available for about half of them. All of these can be regarded as rare and declining; several are close to extinction. Given that record, the remaining species in this range-size category whose current status is unknown deserve emphasis in any regional or global assessment of flying fox conservation.

Restrictive Habitat Requirements: Islands Within Islands

Realistic assessment of range area for species with apparently large ranges rather vaguely defined by scattered museum records requires some knowledge of habitat utilization, as well as habitat distribution. For example, *P. leucopterus* is known from several islands in the Philippines, with a total

area of 107,930 km^2, but this species seems to occur only in high montane forest, a small fraction of this area (Heaney et al. 1987; Heaney and Heideman, unpublished report). Species ranges may be restricted by dependence on habitats with limited natural distributions or, increasingly, because formerly extensive habitats have been altered by man. Coastal and lowland rainforests are among the habitats lost first to timber harvest and agricultural conversion. Flying fox species dependent on primary forest have declined substantially in areas such as Australia and the Philippines, where forest clearance has been extensive (Ratcliffe 1931; Heaney and Heideman 1987). Where primary forest is altered to agroforest rather than replaced by annual row crops or pasture, species which exploit secondary forests may have increased opportunities for range expansion. At least some of the naturally widest-ranging *Pteropus* species, such as *P. tonganus* and *P. giganteus*, forage extensively in agroforest and secondary forest.

How restrictive habitat requirements interact with other factors affecting species survival is illustrated by a small nectar-feeding flying fox, *Notopteris*, found in New Caledonia, Vanuatu, and Fiji (two 19th century specimens of *Notopteris* from Pohnpei are almost certainly locality errors [Andersen 1912; Johnson 1962]). At first glance, this genus seems to have a fairly extensive range which should provide a buffer against habitat alteration in a number of sites. Indeed, since *Notopteris* feeds readily at banana flowers (Medway and Marshall 1975), clearing and planting garden plots may significantly increase its food resources. However, *Notopteris* seems to have restrictive roost site requirements. Colonies are found only in caves and, occasionally, hollow trees. Additionally, residents near Hiengene, New Caledonia, indicated the bats occupied only one of 300 caves nearby (Sanborn and Nicholson 1950). Concentration at well-known traditional sites makes *Notopteris* highly vulnerable to disturbance or exploitation for food. Commercial banana cultivation for overseas export could significantly increase the risk to *Notopteris*. Small scratches on developing bananas made by the claws of flower-visiting bats can reduce crop value because of stringent cosmetic standards for export. In the southern Philippines, pesticides are used in attempts to control flower-visiting bats (N. Ingle, personal communication).

Recent status information gives cause for concern. Though *Notopteris* was caught at virtually all mistnetting sites in surveys in the 1950's in Vanuatu (Medway and Marshall 1975), none were encountered, despite directed searches of caves, in several weeks of recent field surveys in New Caledonia and Vanuatu (T. Flannery, personal communication). It is still numerous in a least one cave on Viti Levu, Fiji (G. Graham and P. Ryan, personal communication).

Unfortunately, we lack the ecological data to define even crudely the habitat requirements of many *Pteropus* species. For most it is safe to say they occupy a fraction of the range circumscribed by the limited available museum records.

The Geographic Scale of Populations

Although species and subspecies are the management units typically recognized in national or provincial regulations and international treaties, in developing local wildlife policy, it is important to recall that the open ocean separating Pacific islands is a barrier to the movement of terrestrial wildlife as well as humans. Flying foxes are obviously more mobile than non-flying terrestrial mammals and have dispersed to many isolated islands. However, the extent of speciation and the morphological divergence among populations on different islands within currently recognized species suggests that long-distance dispersal events are fairly rare. Flying fox species vary considerably in behavior, body size, and wing design, all of which may affect the ability or propensity to fly long distances over open water. This biological background interacting over time with regional geography and weather (storm frequency, wind patterns, etc.) presumably have shaped local patterns of flying fox diversity. In Vanuatu, *P. anetianus* is seemingly comprised of a number of morphologically well-differentiated subspecies on islands separated by only moderate distances, while morphological differences among populations of *P. t. tonganus* separated by several hundred kilometers are slight (Felten 1964b; Felten and Kock 1972; Wodzicki and Felten 1980).

Shifting back from an evolutionary to a management perspective, morphologically distinct populations on different islands, whether currently recognized as subspecies or not, generally offer a basis for practical management units. A more difficult task is identifying biologically meaningful management units within morphologically homogenous species that occur on several islands. This may be particularly important if adjacent jurisdictions have differing pressures on wildlife populations. For example, Wiles (1987a; personal

communication) reported that in the remnant population of *P. m. mariannus* on Guam (protected as an endangered species) no young survive predation by the introduced brown tree snake. Persistence of the population in this demographic sink is apparently maintained by periodic movements of flying foxes to and from Rota Island across 60 km of open water (Wiles and Glass 1990). The flying fox population on Rota is monitored, but is subject to substantial legal and illegal hunting, and efforts at both enforcement and stricter statutory protection have not been politically viable (Wiles et al. 1989; Lemke 1990). Wiles and Glass (1990) showed that a biologically meaningful management unit includes both Guam and Rota. The near-term fate of the flying fox population on Guam is inextricably linked to de facto wildlife policy in the CNMI.

The wide total range of *P. mariannus* and *P. tonganus* suggests they fall near the upper bound for dispersal capability in Pacific *Pteropus*. In the absence of band recovery data or genetic analysis, a reasonable preliminary hypothesis is that island populations separated by 100 km or more of open ocean will not experience movements of flying foxes sufficient to substantially influence population size and should offer a basis for local management units.

Implications of the Archaeological Record

The continuing work of D. Steadman and other workers (Steadman 1989) on faunal remains in archaelogical sites, particularly in Polynesia, but also elsewhere in the Pacific, reveal that modern avifaunas on most islands are a small subset of the community present when humans first arrived. He coined the term "pseudo-endemic" for species whose current, very limited geographic ranges result from human-induced extinctions on other islands. At present the only evidence of pre-European extinction of flying foxes comes from 'Eua, Tonga, where a species allied to *P. samoensis* and a small nectarivorous pteropodid are part of a larger assemblage of vertebrates (Koopman and Steadman, personal communication) whose extinction occurs after the Polynesian occupation. As Steadman (1989) noted, the process of avifaunal extinction continues unabated.

While additional archaeological data may reshape this perception, it seems that the rate of extinction of island flying foxes has accelerated in the era since European contact. As detailed elsewhere in this volume, improved hunting technologies, changing cultural patterns of resource consumption, accelerated habitat alteration, and the introduction of alien species have all played a role. The ecological consequences of the recent loss of these species is unknown. Among the remaining taxa, those with limited ranges and restrictive habitat requirements are generally at greatest risk.

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Appendix. Megachiropteran references by country.

Selected references to literature (published or in press before this volume) on megachiroptera occurring in Pacific island nations or territories are indexed below. The selection emphasizes more recent references on distribution, systematics, ecology, and conservation status, providing a starting point for broader investigations. Morse et al. (1987) provide a general bibliography of recent references on the Megachiroptera.

American Samoa: Cox 1983, 1984; Wodzicki and Felten 1975.

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Guam: Wiles 1987a, 1987b; Wiles and Payne 1986; Wiles et al. 1989.

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Commonwealth of the Northern Marianas: Lemke 1986; Wheeler 1980; Wiles et al. 1989; Wiles and Payne 1986.

Federated States of Micronesia: Bruner and Pratt 1979; Falanruw 1988; Jackson 1962; Johnson 1962; Ralph and Sakai 1979; Wiles et al. 1991.

Japan (Ryukyu, Bonin, and Volcano Islands): Ishii 1983; Yoshiyuki 1989.

New Caledonia: Felten 1964b; Sanborn and Nicholson 1950.

Niue: Wodzicki and Felten 1975.

Palau: Engbring 1983; Perez 1968; Wiles and Conry 1990; Wiles and Payne 1986.

Papua New Guinea: Flannery 1989, 1990; Koopman 1979, 1982.

Philippines: Heaney and Heideman 1987; Heaney et al. 1987; Heideman and Heaney 1989; Koopman 1989; Musser et al. 1982.

Solomon Islands: Felten 1964a; Flannery 1989; Hill 1956; Phillips 1968; Sanborn and Nicholson 1950.

Tonga: Gill 1987.

Vanuatu: Baker and Baker 1936; Baker 1947; Chambers and Esrom 1988; Felten 1964a; Felten and Kock 1972; Medway and Marshall 1975; Sanborn and Nicholson 1950.

Western Samoa: Cox 1983, 1984; Wodzicki and Felten 1975.

Fruit Bats of Vanuatu

by

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Introduction

Two reports cite the general distribution and status of flying foxes in Vanuatu (Medway and Marshall 1975; Chambers and Esrom 1988). There has never been any attempt, however, to assess the numerical status or detailed distribution of flying foxes in Vanuatu.

Distribution and Status of Flying Fox

Flying foxes, until recently, were distributed in the Pacific, from Palau and Guam in the north, the Cook Islands in the east, and Papua New Guinea in the west to Vanuatu in the south. Recently, within much of this range, flying fox numbers have drastically decreased, and in many areas they are now extinct. Declines were caused by overhunting, natural disasters (e.g., cyclones), and destruction of forest cover by logging companies and subsistence farming.

Flying foxes are also present in the Solomon Islands, Fiji, Tonga, New Caledonia, the islands of the Federated States of Micronesia, and the Commonwealth of the Northern Marianas.

Throughout this wide range, flying foxes are considered threatened (Convention on International Trade in Endangered Species of Wild Fauna Flora [CITES] 1989). In many countries flying foxes are legally protected and intensively studied so that policies may be implemented for their conservation. In Vanuatu, there is no specific legislation that forbids the capture of flying foxes.

The Vanuatu Archipelago

The Vanuatu archipelago consists of a Y-shaped chain of 80 islands (70 inhabited in 1979) situated between about latitudes 13–20° S and longitudes 166–170° E (Figure). The total land area is 12,190 km^2, of which the largest island, Santo, has an area of 4,248 km^2. The population of Vanuatu is about 140,000 (1986 estimate), with about 80% leading a traditional way of life. Shifting agriculture provides most food and is supplemented by hunting and gathering from reef, river, and rainforest.

Climate

The climate of Vanuatu varies considerably along the length of the archipelago. In the north, conditions are hot and humid with little seasonal variation. In the south, temperatures and rainfall are lower (Table 1), and seasonality is much more pronounced.

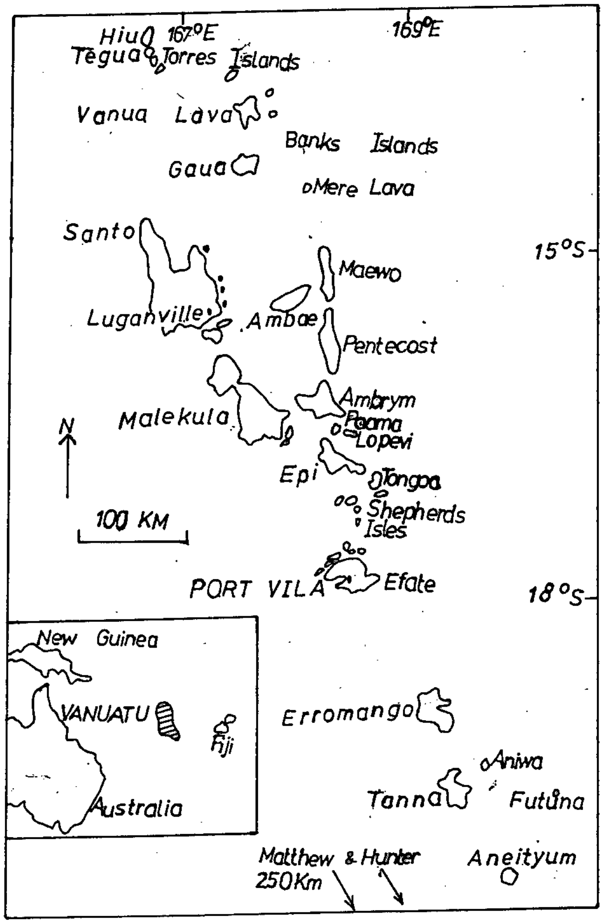

Figure. Major islands and island groups of Vanuatu.

Table 1. *Rainfall and temperature data for selected localities in Vanuatu (30 year averages to 1987).*

Locality	Annual rainfall (mm)	Mean Monthly max. temp. (° C)	Mean Monthly min. temp. (° C)
Vanua Lava	4,210	29.2	23.3
Port Vila	2,270	28.7	21.6
Aneityum	2,155	27.1	20.5

Vanuatu lies in the cyclone belt and is subjected, on average, to 2.6 cyclones per year. Generally, each island is struck by the full force of a cyclone about once every 30 years, but stormy winds associated with the edges of cyclones are common occurrences at all localities.

Prevailing winds on Vanuatu are generally from between the east and southeast—about 80% of all recorded wind directions. Strong winds, however, particularly those associated with cyclones, may come from any direction.

Mammals of Vanuatu

The only mammals found in Vanuatu are bats and rats, of which only bats are native. The islands' youth and isolation prevented all animals except bats from arriving here by themselves. There are 12 species of bats—4 fruit bats and 8 Microchiroptera. The most recent account is by Medway and Marshall (1975); there is a need for more research.

The species of fruit bats are *Pteropus tonganus* (black flying fox), *P. anetianus* (white flying fox), and the two common species, *Pteropus fundatus* (recorded from the Banks Islands in northern Vanuatu) and *Notopteris macdonaldi* (long-tailed fruit bat). *Pteropus anetianus* is endemic, and seven subspecies have been described, indicating perhaps that it is a rather sedentary species (Chanbers and Esrom 1988).

Pteropus tonganus, *P. anetianus*, and *N. macdonaldi* coexist throughout much of the archipelago. Competition seems to be reduced or avoided by their different roosting and feeding habitats. *Pteropus tonganus* lives in large colonies in large trees, particularly the giant tree of the forest—the banyan—and is essentially a fruit-eater. *Pteropus anetianus* lives in smaller groups in smaller trees, especially coconut trees, and is chiefly a flower-eater. *Notopteris macdonaldi* lives in caves and is nectarivorous (Chambers and Esrom 1988).

Questionnaire Survey

In October 1988, the Environmental Unit of the Ministry of Lands, Geology, Minerals, and Rural Water Supply conducted a questionnaire survey during the annual workshop of the field workers of the Vanuatu Cultural Center, held in Port Vila. This workshop was an excellent opportunity to conduct the survey, considering the cost of administering it throughout the archipelago.

The Cultural Center field workers are men with considerable knowledge, expertise, and interest in the cultural affairs of Vanuatu. A short questionnaire was prepared for them, and it is the analysis of 28 completed forms that provided some information on the cultural and social importance of flying foxes of Vanuatu.

Out of the 35 forms distributed, 28 (80%) were returned by the end of the meeting. The results were fairly uniform for all the islands and local cultures represented in the replies. One of the four species occurring in Vanuatu *(Pteropus tonganus)* is the most common everywhere; nearly everyone eats it, and it is an important animal in local diets. The study revealed many interesting beliefs and stories about flying foxes. Apart from their food value, they are clearly animals of significant cultural importance.

All the field workers said the people of their villages killed and ate fruit bats, and 85% of them said bats were an important component of their diets. There were many methods of capture reported—bows and arrows, guns, sticks, stones, catapult, hooked strings, and nets. Sticks are used as missiles to knock the bats to the ground, and hooked strings are laid across likely feeding places and pulled sharply to catch the bats. The bats are caught mainly while feeding on banana, papaw, or other fruit trees. With the exception of the gun, virtually all methods of capture can be considered as traditional (Chambers and Esrom 1988).

Despite this regular hunting, most people (75%) said that bat numbers remained stable or had increased. There is no evidence that hunting at existing levels reduces bat numbers. Large numbers of bats are killed during cyclones, which strike Vanuatu regularly.

Local Language Names

Vanuatu has 105 distinct local languages. Most field workers gave their local language names for both *P. tonganus* and *P. anetianus*, while two also gave the name for *N. macdonaldi* (Table 2). In a few cases, it was not stated to which flying fox the given name referred. Most likely the name referred to *P. tonganus*, as this seems to be the most common species, near the villages at least. No specific information was provided on the roosting sites in the survey, but these are believed to be in areas away from villages. No current population estimates of flying foxes are available, but numbers are suspected to be increasing throughout the archipelago.

Protected Status

Vanuatu has no specific legislation that forbids the capture of flying foxes, but the exploitation of some animal and plant resources is regulated by traditional laws. However, few such controls operate for fruit bats in Vanuatu. Thus, most people catch and eat them. Some exceptions were mentioned: one group considers fruit bats their ancestors, and does not eat them; Seventh day Adventists regard them as evil; and women are banned from catching fruit bats in one village, because it is believed that they would exterminate the resource.

On 15 October 1988, Vanuatu became a party to the Convention on International Trade in Endangered Species of Wild Fauna and Flora, and the International Trade (Fauna and Flora) Act for Vanuatu was introduced and passed in parliament in 1989. These laws ban international trade of flying foxes from Vanuatu.

Fruit bats are usually only killed for food. In only three cases were they taken for sale. In Vanuatu's capital, Port Vila, flying foxes are occasionally sold, and they sometimes are on the menus of tourist hotels. On the whole, however, the bats seem to provide little cash income for villagers. Fruit bats are rarely exported and always in small numbers.

Many replies from the questionnaires related traditional stories about fruit bats. These stories show a strong relation between fruit bats and traditional beliefs. As noted above, in several areas people consider black flying foxes as their ancestors. Such people have a special bond with the bats and are able to communicate with them. This power may be frequently used to persuade the bats to attack other people's fruit gardens and to avoid one's own—or so the stories are told.

The flying fox also appears in the traditional art of sand-drawing. In this art, the design is drawn in one continuous motion by fingers tracing out the intricate and geometric designs on the ground or sand.

Conclusion

In Vanuatu, fruit bats are important animals. They are a cheap and readily available form of protein for most people. Present hunting levels do not seem to be causing any reduction in numbers. If there is any threat, at least to local bat populations, it probably comes from cyclones. Large numbers of bats may be blown to the ground, during cyclones, then they are killed by the villagers. Even when not killed, they are unable to fly.

Table 2. *Local language names of flying foxes in Vanuatu. Names in parentheses indicate that it was not certain to which flying fox the given name referred. In most cases, however, the name probably referred to* Pteropus tonganus.

Locality	*Pteropus tonganus* Black flying-fox	*Pteropus anetianus* White flying-fox	*Notopteris macdonaldi* Long-tailed fruit bat
Ambrym			
Lonmei	Gelei ten	Gelei berass	
Ranon	Genei kon	Genei pera	
Sameo	Makon	Veres	
Aneityum			
Anpekeh	Nekrae	Nalvahan	
		Nekrasyaij	
		Nauodelcau	
Efate			
Erakor	(Mantu)		
Epi			
Lamen Island	Menki	Mberu	
Erromango			
Pongkil	(Nagkarai)		
Umpon	Nankarai	Nomporpor	
Yelongi			
Futuna			
Ipao	Beka		
Malakula			
Lawa	Nemen Kerai	Nawusmo	
		Netomboras mave	
Lorlow	Namen kahai	Nawusmo	
Pellonk	(Mankulai)		
Wala Island	Kramot	Lewot	
Wintua	Nemenbasboni	Nevibow	
	Nemengeri		
Vao Island	Kere Meuk	Kere meul	
Malo			
Avunatari	Manu	Wondae	
Nguna			
Tikilasoa	Manutua	Mantua pakku	
		Manuva	Mantuatau
Pentecost			
Loltong	Mangogona	Bwaragogo	Geregeihi
Ranputor	(Bwaras)		
Santo			
Nokuku	Mankonkon	Tovut	
Wusi	Takilekile		
Tanna			
Isakwai	(Kei)		
Itonga	(Kei)		
Vanua Lava			
Veutumboso	Qeret Korkor	Toqol	Menrukruk

Flying foxes are important in custom and tradition. People from several areas believe themselves descended from flying foxes, while in some areas the flying fox is credited with the origin of men.

In some areas the flying fox is regarded as a pest because of the damage they do to fruit crops. Thus, the relation between man and flying fox is not always beneficial or harmonious.

The most serious threat to flying foxes, as well as to bird species in Vanuatu, is clear-cutting of forest for conversion to agriculture and human settlements, particularly on very populated islands.

More detailed studies of flying foxes and their importance to Vanuatu are required, as is specific protective legislation.

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The Moa Kirikiri of the Cook Islands

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The islands of Mangaia and Rarotonga in the Cook Islands are the most eastern localities of flying foxes in the Pacific (Wodzicki and Felten 1981). The Cook Islands consist of 15 islands in a remote section of the South Pacific Ocean. The islands are between Tonga and Samoa to the west and French Polynesia to the east. These islands are divided into a northern group of six islands and a southern group of nine islands, including Mangaia and Rarotonga.

Pteropus tonganus is the only species of flying fox in the Cook Islands (Wodzicki and Felten 1981). Frequently referred to as the Tongan flying fox, it is more commonly known to our people by its traditional name—Moa Kirikiri, which probably means "fowl with leather skin." Moa Kirikiri was introduced to Rarotonga from Mangaia in the 1870's. How, why, and by whom are unknown. The flying fox was on Mangaia in pre-European times, although it is not known whether it is native or was aboriginally introduced. These bats appear in uninhabited areas of the Makatea cliff that circles Mangaia and in the rugged, forested mountains of central Rarotonga (Wodzicki and Felten 1981).

Moa Kirikiri include at least 18 species of plants found on the Cook Islands in their diets (Wodzicki and Felten 1981). This list of vegetation includes native and introduced species. During the southern winter months of June, July, and August, these bats eat blossoms from kapok (*Ceiba pentandra*; Wodzicki and Felten 1981) and *Cecropia palmata* trees. Similar plants are used by *P. tonganus* on Niue Island (Wodzicki and Felten 1975). The trees that bats preferred for roosting all have sparse leaves and widely spaced branches (Wodzicki and Felten 1981).

Moa Kirikiri gives birth soon after kapok trees bloom (Wodzicki and Felten 1981). During this time, the bats are fat and are considered a delicacy by the local people who hunt and eat them. Hunting pressure during the reproductive season has apparently caused a reduction in the flying fox population (Wodzicki and Felten 1981). Although no surveys have been conducted in the Cook Islands, rough estimates indicate that there may be 500 to 1,000 bats on Rarotonga and a similar number on Mangaia. There are no local laws that regulate the hunting of flying foxes on the Cook Islands.

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Part 4.

Policies and Protection

Local Policies and Protection by the Government of Guam

by

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Introduction

Background

The fruit bat (*Pteropus mariannus mariannus*) plays an important part in the culture of the Chamorros, the indigenous population of Guam. Fruit bat is a prized native food item, and a host will proudly serve it at a party table even if the quantity is small. The objective is to show off to the guests rather than an attempt to satisfy their appetites. This is an incongruity on the part of the Chamorro host, as it is considered bad form to run out of food at a party. In fact, the Chamorros have a saying, "Maolekna sopbla kinu tinahong nenkanno," which translated means, "It is better to have leftovers than not to have enough food." However, the transgression of cultural values is acceptable when serving scarce food items and this, in fact, enhances the status or prestige of the host.

The Marianas fruit bat was not always scarce. When I was a child, my father told me stories of the fruit bat being so abundant that hog raisers in outlying areas in northern Guam used to catch them and feed the cooked fruit bats to their pigs when breadfruits and other native and cultivated plants were scarce. I also heard stories of the ease by which fruit bats were caught by scooping them from the air with a net.

This may have been true during my father's time, as he was born in 1904. In that era Guam was undeveloped, the human population low, and the forests pristine. Unfortunately, Guam's human population has grown dramatically since the turn of the century, increasing from 9,701 residents in 1901 to 22,000 in 1940 to 106,000 in 1980 (Wiles 1987).

Wheeler (1979) stated that, "In 1957 a U.S. Fish and Wildlife Service biologist visited Guam to determine the feasibility of initiating a wildlife program. He estimated the fruit bat population on Guam to be not more than 3,000 bats. . . ." During fiscal year (FY) 1957, Guam became eligible for participation under the federal aid programs for sport fish and wildlife restoration (Lowe 1958). Fiscal year 1958 was the birth year for the precursor of the Division of Aquatic and Wildlife Resources of the Department of Agriculture, Government of Guam (Lowe 1958). It was not until FY 1963, however, that a study of the fruit bat was initiated (Guerrero 1963).

The enactment of Public Law 8-43 in 1965 removed the fruit bat from the list of unprotected wildlife (Guerrero 1966; Wiles 1987). Regulations were promulgated in 1966 making the fruit bat a game animal and establishing a 44-day fruit bat season. Only 8 fruit bats were reported caught that year (Guerrero 1966). In FY 1967, 40 fruit bats were caught during the legal hunting season. Wiles (1987) reported that, "During succeeding years, the length of seasons and bag limits became more restrictive as bat numbers continued to decline. Finally, all hunting was prohibited in 1973 (Wheeler 1979). . . ." In 1971 and 1972, the division recommended, without success, the closing of the fruit bat season until the fruit bat population recovered (Wheeler 1979).

The fruit bat has been protected as a game species since 1966 and from all legal hunting since 1973; however, the illegal taking or hunting of fruit bats has continued to be a problem (Perez

1972; Wheeler and Aguon 1978; Wheeler 1979; Wiles 1987). The lack of an adequate number of enforcement personnel has continued to plague the Division of Aquatic and Wildlife Resources. Recommendations have been made since 1973 to increase the number of conservation officers in order to increase enforcement effort to control poaching. It was not until 1981, however, that the local legislature provided funds for the hiring of an additional conservation officer, increasing the total enforcement force to six (Aquatic Wildlife Resources 1981).[1] In FY 1985, the local legislature appropriated funds to allow for two new conservation officer positions, bringing the number of enforcement personnel to eight (Aquatic Wildlife Resources 1985). Between FY 1980 and FY 1984, funding was provided by the Coastal Zone Management Program for the hiring of personnel on a nonpermanent basis to augment the permanent enforcement force; this ranged from a low of one in FY 1980 to a high of three in FY 1981 (Aquatic Wildlife Resources 1980–1984).

The initial request to list the fruit bat as an endangered species was made to the Secretary of the Interior by the Governor of Guam on 28 August 1978. On 18 May 1979, the U.S. Fish and Wildlife Service (Service) published a notice in the *Federal Register* for the "... review of the status of ... two mammals from Guam" (U.S. Fish and Wildlife Service 1979). The notice requested additional data as well as information that could lead to "Critical Habitat determination ...." (U.S. Fish and Wildlife Service 1979). On 29 November 1983, the Service published a proposed rule to designate the fruit bats (*P. m. mariannus* and *P. tokudae*) as endangered species. The Service found that "... designation of Critical Habitat is neither prudent nor determinable at this time" (U.S. Fish and Wildlife Service 1983). On 27 August 1984, the fruit bats were officially listed as endangered (U.S. Fish and Wildlife Service 1984). This listing under the U.S. Endangered Species Act provided additional protection to the fruit bats, which had been listed as endangered under the Guam Endangered Species Act in 1981 (Wiles 1987).

On 28 August 1987, Governor J. F. Ada, of Guam, petitioned the Director of the Fish and Wildlife Service, "to designate critical habitat for ... 2 bat species" (Governor J. F. Ada, personal communication). Governor Ada stated that, "Conditions since the original listing have changed considerably and we now believe that designation of critical habitat is both prudent and necessary ...." The director responded to Governor Ada on 23 September 1987, informing him that "... the Service will promptly conduct a review of the situation and take appropriate action." On 16 March 1988, Governor Ada wrote to Secretary of the Interior petitioning to "... designate critical habitat for these species under the Emergency Rule provisions of 50 CFR 424 20 [sic]."

On 19 May 1988, the Nineteenth Guam Legislature adopted Resolution 339 entitled, "Relative to requesting the Secretary of Interior to issue an Emergency Rule designating critical habitat for the endangered forest birds and fruit bats of Guam." This resolution was cosponsored by all 21 members.

On 27 February 1989, Governor Ada was informed by the Director of the Fish and Wildlife Service that "The Service agrees with the merits of your petition that critical habitat may be beneficial for six of the species .... Such a designation would protect important forest habitat necessary to support the recovery of these six species .... In addition, the Service will aggressively pursue positive measures to control the exotic brown tree snake, whose presence has had major influence on the depletion of native vertebrates on Guam ...." (F. Dunkle, personal communication).

On 2 June 1989, Service representatives met with representatives from the government of Guam for an informal discussion on critical habitat, the process, and implications.

On 4 October 1989, the Director of Agriculture, Guam, submitted a revised critical habitat map to the Director of Bureau of Planning. The revised map excluded areas not essential or critical to the continued existence of the endangered species.

Discussion

The government of Guam through the Department of Agriculture's Division of Aquatic and Wildlife Resources (DAWR) has been monitoring fruit bat populations since the early 1960's (Perez 1972; Wheeler and Aguon 1978; Wheeler 1979; Wiles 1987). Perez (1972) reported on the general decline of Guam bats based on surveys conducted from 1962 to 1968 by staff of the predecessor of DAWR.

[1] Aquatic and Wildlife Resources Division, 1980–1985. Job progress report — federal aid to fish and wildlife restoration, Guam. Department of Agriculture, Agana, Guam 96910.

It was presumably from these studies that fruit bats were taken off the list of unprotected wildlife in 1965 and regulated as a game species from 1966 to 1973 (Guerrero 1966; Wheeler 1979; Wiles 1987).

Fruit bats have been protected since 1973 (Wheeler 1979). Additional protection was afforded to the fruit bat in 1981, when it was placed on Guam's Endangered Species List, and in 1984, when it was placed on the U.S. Endangered Species List (Wiles 1987).

The Fifteenth Guam Legislature passed Bill 375, known as "The Endangered Species Act of Guam." This bill was enacted into law on 18 June 1979 as Public Law 15-36. This act provided, among other things, authority to the Department of Agriculture to regulate, conduct research, and promulgate a list of endangered species. There were some flaws in this act, and it was subsequently amended by Public Law 15-97 in 1980.

While it has been postulated that the decline of the fruit bat was because of illegal hunting and habitat destruction, the role of the brown tree snake (*Boiga irregularis*) in the decline of the fruit bat has not been fully analyzed. Fritts (1988) reported that "The brown tree snake was first detected in the Santa Rita area near the Naval Port, but snakes may not have become conspicuous until the early 1960's . . . . By the mid-1960's, the snakes had colonized over half the island's area. . . . In 1968, the snake had reached the extreme northern end of the island . . . and was probably present throughout the island." Perez (1972) reported that "Unlike NCS and Tarague, where the frequency index showed fluctuations of under 20%, . . . bat observations at Fena Lake dropped from a five year average of 100% to 54% in 1968. . . ." ([The Naval Communication Station] and Tarague are on the northern end of the island, which was not reached by the snake until 1968. Fena Lake is located in south-central Guam.) Wiles (1987) reported that "the brown tree snake appears capable of preying on bats. . .one case of snake predation has been reported. A local resident related finding a 2.5-m-long snake with three young fruit bats in its stomach. . . . The brown tree snake may be more directly involved in the post-World War II declines of bats in southern and central Guam than originally thought."

Recent efforts by DAWR to protect and conserve the fruit bat include planning for snake-proofing trees where fruit bats roost, requesting the preservation of public lands that are suitable habitats for the fruit bat, and requesting funds to hire additional Conservation Officers. Work is now progressing on the investigation of barrier and trap designs that will prevent snakes from getting into fruit bat roosting trees.

The importation of fruit bats into Guam requires a permit. This has been a requirement by the Government of Guam since the mid-1960's. The enforcement of this policy is carried out by Customs and Quarantine Officers of the Guam Department of Commerce.

Recent Development

The amendment to the Convention on the International Trade in Endangered Species of Wild Fauna and Flora Treaty (CITES) is of concern. The inability to import fruit bats into Guam may subject Guam's fruit bats to greater illegal hunting pressure (Wiles 1987). Our goal is to manage the fruit bats as a game resource and to implement management and conservation measures.

Recommendations

The following actions are recommended to prevent the extinction of the fruit bat:

1. Continue existing studies on fruit bats;
2. Increase enforcement efforts and seek additional funds to hire more enforcement personnel;
3. Investigate the impact of the brown tree snake on the fruit bat;
4. Control or eradicate the brown tree snake;
5. Conserve and protect fruit bat habitat;
6. Increase public information and education efforts on the fruit bat;
7. Continue the permit requirement for the importation of fruit bats; and
8. Remove fruit bats from Appendix I of CITES in areas where they are not threatened or endangered, and manage the bats as a game resource with appropriate management and conservation measures. (The objective of this particular recommendation is to provide alternate sources of fruit bats to prevent more pressure by illegal hunting on the Marianas fruit bat.)

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History of Fruit Bat Use, Research, and, Protection in the Northern Mariana Islands

by

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Abstract. Marianas fruit bats, *Pteropus mariannus*, have an esteemed place in the local Chamorro culture as a special food item. From prehistoric times fruit bats have been important to this food-oriented society that values dietary variety. Since 1521 the Chamorro culture was systematically destroyed by four Western civilizations and an influx of Micronesian races. While other Micronesian cultures have maintained aspects of their pre-contact heritage such as art, folk dance, traditional dress, class distinctions, navigational skills or social customs, few Chamorro traditions have survived. The Chamorro language and custom of eating bats are a few of the cultural remnants left. Since the 1970's fruit bat populations in the northern Mariana Islands have seriously declined because of commercial hunting for human consumption. A number of conservation efforts have had limited success. Even in the face of fruit bat extinctions local residents demand an opportunity to hunt bats and enjoy this cultural delicacy. Future efforts to save fruit bats must address the history of complex social, biological, and political issues.

In the last decade scientists have focused attention on the Marianas fruit bat (*Pteropus mariannus*) or "fanihi," as it is known in the Chamorro language, on the 14-island archipelago of the Commonwealth of the Northern Mariana Islands (CNMI). Fruit bats on these islands and on neighboring Guam have drastically declined in numbers and face threats to their survival. Their future as an extant native species is uncertain. Bat populations are almost gone on the islands of Saipan, Tinian, and Aguijan, while the population on Rota continues to receive significant illegal harvest (Wiles et al. 1989). Fruit bats on the islands north of Saipan are protected, to some extent, by their remoteness but still face poaching problems.

Important decisions regarding the future of fruit bats in the CNMI will probably be made within the next decade. Internal and external interests are now directed toward the management and preservation of this unique species. A regional Pacific-wide approach to fruit bat conservation may transpire in the near future (Bat Conservation International 1990). In light of recent events, it is appropriate to understand the importance of fruit bats in the Chamorro culture and to review research and conservation history.

Problems that face fruit bat conservation in the CNMI are more complex than casual observations reveal. It is important to recognize why fruit bats are immensely sought after and to understand what factors continue to jeopardize their

existence. Suitable solutions must address and answer biological, social, and political concerns.

History and Use of Fruit Bats in the Marianas

Island History and Fruit Bats

The first people to inhabit the Mariana Islands are thought to have arrived around 1500 B.C. (Thompson 1932). They were very likely a race of people with a Malaysian or Polynesian ancestry who arrived by sailing canoes. Early settlers developed into the Chamorro culture organized into matrilineal clans living in small villages ruled by local chiefs. People lived by gardening, food gathering, and fishing with the aid of ingenious technology. Most notable was the construction of latte, or large stone pillars, at house and canoe shed sites (Thompson 1945).

The archeological record from Rota indicates that fruit bats were hunted and eaten by early Chamorros at least 2,500 years ago, and Thompson (1945) listed bats as an important food source in her monograph on ancient Chamorro culture. There is no record of cultural food laws regarding bats, although there were seemingly three distinct social classes. Elsewhere (Yap Islands), the eating of fruit bats was relegated to lower-class people who had no access to marine resources (Falanruw 1988).

Magellan discovered the Mariana Islands for Spain in 1521. Foreign rule quickly destroyed Chamorro society. The Spanish decimated Chamorro populations and culture in the process of converting natives to Christianity and western civilization. The conversion process included 30 years of bloody fighting, introduced epidemics, and removal of all natives from the islands north of Guam (Hezel and Berg 1984). An estimated population of 100,000 Chamorros in 1668 was reduced to a censused population of 3,678 Chamorros on Guam in 1710 (Thompson 1945). During the next century, extensive mixing with Spaniards, Filipinos, and other island races eliminated much of the Chamorro bloodline and local traditions (Villagomez 1981). Following Spanish rule, the northern Marianas were administered by Germany (1899–1914), Japan (1914–45), and the United States (since 1945), which further influenced native customs (Hezel and Berg 1984).

Fruit Bats as Food

Throughout the Pacific region, Chamorros are renowned for their use of fruit bats as food. The eating of bats is one of the few Chamorro customs that dates back to pre-Hispanic times and thus takes on additional significance. Social events revolve around the consumption of a large variety and amount of food. Great care is taken in the preparation and presentation of food, particularly native dishes from the sea, the forest, and local gardens. The social status of families is judged by the variety and amount of foods served at events such as weddings, birthdays, and important religious holidays.

Fruit bats, because of their distinct taste, odor, and perhaps rarity, top the list of desirable food items to serve at special occasions. When fruit bats are prepared, none of the animal is wasted. Recipes implore that bats do not require skinning or eviscerating, simply washing the fur is sufficient (Rody 1982). Bats are often boiled in a seasoned soup with coconut milk added. The fur, meat, viscera, and wing membranes are eaten. The dark meat has a distinctive "gamey" taste, and the bats produce a distinct musky odor while being prepared. Some recipes indicate that one bat will serve two adults; however, in recent times, one bat may be served to several people. With the scarcity of fruit bats, consumption is limited to the oldest and most respected family members or special guests. Fruit bats are a delicacy and not a staple in the modern diet.

Fruit Bat Hunting Methods

Before the use of firearms, bats were harvested with nets, traps, and primitive weapons. Long-handled scoop nets were used to capture individual bats as they fed in trees or flew along well-used routes (Safford 1902). Long, elaborate nets suspended above the ground were used to catch large numbers of bats along major flyways. Sticks with thorn branches attached were used to hit and entangle bats as they fed in trees (D. Aldan, personal communication). Stones, either hand thrown or launched from a sling, were used to take individual bats at close range. Considerable patience, skill, and knowledge of bat behavior is required to take animals using primitive methods. As recently as the 1960's, individuals were respected for their abilities to harvest bats using the old ways.

Firearms came to the Marianas by way of the Spaniards in 1521. Chamorros discovered the power of firearms when seven natives were shot and killed by Magellan's men during an early encounter (Hezel and Berg 1984). It would be over 400 years before the general population had access to firearms and before they were used in hunting. The Spanish, German, and Japanese administrations prohibited locals from owning guns. Bats taken during this period were largely captured using the old methods. After the Japanese were defeated in 1945, the U.S. Navy and U.S. Trust Territory loosened legal restrictions regarding firearms. Since the 1950's, the main factors in obtaining a gun are the supply of firearms and the ability to afford one.

The modern hunting weapon of choice for fruit bats is a shotgun with birdshot loads of number 6, 7½, or 8 shot. Pellet guns and .22 rifles are occasionally used to shoot roosting bats. In the CNMI, civilian arms are restricted to .22 caliber or smaller rifles and nothing larger than .410 shotguns. Pistols are prohibited for civilian use. All guns must be registered, and legal proof is required to purchase ammunition. Violations of the firearms laws carry severe penalties. Federal laws in the 1960's, which ended the sale of guns through the mail, reduced the purchase of weapons in the Pacific islands. Firearm dealerships are now slowly increasing in the CNMI. Major retail stores sell guns and ammunition. The cost of firearms and ammunition is about twice that of similar products on the U.S. mainland. Owing to the .410 gauge restriction, most shotguns in the CNMI are single-shot models. Over and under .22/.410 models are also popular and practical.

The preferable way to shoot bats is at the roost site. Typically, a small number of hunters quietly approach a colony and fire simultaneously at roosting bats. In the confusion, each hunter may fire several shots as bats attempt to escape. Several bats can be killed with one shot (Nicholson 1945).

Bats are also shot at known feeding sites and along flyways. Shooting flying bats in dim light is difficult. Most hunting, especially poaching, occurs at night or under poor light conditions. The difficulty of finding downed bats in thick vegetation can result in significant retrieval loss. Some hunters on Rota have successfully used dogs to retrieve fruit bats (A. Ramos, personal communication). Hunting at nursery colonies may cause abandonment or direct mortality of infant bats.

Bat Research

The first survey of fruit bats in the CNMI was conducted on Rota in January 1977 by biologists from Guam Aquatic and Wildlife Resources (GAWR; Wheeler 1979). During the 2-day survey, one colony of 100–150 bats was located. The intent of the trip was to capture and radio-collar bats for a natural history study. Bat populations on Guam were already too low to make capture efforts likely. The Rota bat population was much lower than expected, possibly because of super-typhoon Pamela, that hit the island in May 1976. The effort to capture bats was canceled.

From 1951 to 1978 the northern Mariana Islands were governed by the U.S. Trust Territory of the Pacific Islands (TTPI), following a short period of U.S. Navy control (1945–51). The wildlife resources of the northern Marianas came under the jurisdiction of one conservation officer, who served the entire territory and was based on Palau (Owen 1969). No fruit bat studies were conducted during the TTPI period.

Incidental to bird surveys in the Marianas, Ralph and Sakai (1979) expressed concern for low numbers of bats on Rota and Saipan during a visit in 1977. They did not observe fruit bats during 13 h of bird surveys that covered 14 km of forest transects. Brunner and Pratt (1979), also incidental to bird surveys, commented on the rarity of fruit bats on Rota and Saipan, where they observed only three bats in 1976.

In 1979, Wheeler (1980) surveyed fruit bats on Saipan, Tinian, and Rota using a combination of survey station and roadside counts, techniques used to survey bats on Guam. Three biologists made observations from 40 different survey locations, selected on the basis of similarity to preferred bat habitat on Guam, and along 298 km of road. The team observed 39 fruit bats on Rota, 2 on Tinian, and 0 on Saipan, with a similar search effort on each island. Based on surveys and local reports, Wheeler (1980) indicated that bats may have been extirpated on Saipan, whereas population estimates were 25 for Tinian and 200–400 for Rota.

In January 1978 the northern Marianas became the U.S. Commonwealth of the Northern Mariana Islands (CNMI). The new political status allowed the CNMI to qualify for Federal funding programs, including the Pittman–Robertson Federal Aid in Wildlife Restoration Program. The Pittman–Robertson Program is funded through fed-

eral excise taxes on firearms, ammunition, and archery equipment. The program is administered by the U.S. Fish and Wildlife Service (Service) to qualifying resource agencies.

In 1981 the CNMI received its first Pittman–Robertson budget to fund the Division of Fish and Wildlife (DFW) within the Department of Natural Resources (DNR) on Saipan. The first two wildlife biologists, hired in 1983, began to work on a variety of projects, including fruit bat surveys and inventories. Fruit bats received high priority because of population declines and high cultural value.

Since 1983, the DFW has conducted fruit bat research on all of the Commonwealth islands, with an emphasis on Rota. The main objectives have been to (1) determine population status and distribution; (2) determine habitat preferences and food habits; (3) investigate productivity, social behavior, and mortality factors; (4) initiate a public education program; and (5) develop management recommendations. Results of those studies appear in a series of unpublished annual reports (Lemke, Schmitt, Glass and Villagomez, and Glass and Taisacan).

In 1983 the DFW helped support and participated in the Oxford University Fruit Bat Expedition (Anonymous 1984). A group of six observers, including DFW and GAWR biologists, attempted for the first time to census fruit bat populations north of Saipan (Wiles et al. 1989). Information on fruit bat habitats was also gathered on this trip (Lemke, unpublished report).

Bat Conservation

Local Laws and Enforcement Efforts

Some islands implemented their own fruit bat hunting regulations at the municipality level, under the TTPI government. In 1970 the municipality of Rota established a fruit bat season from 1 September to 31 December, with no bag limits (Wheeler 1979). However, fruit bat hunts occurred at other times of the year when authorized by the Mayor of Rota. The municipality of Tinian created hunting regulations and established a wildlife sanctuary on the island of Aguijan. There was little enforcement of the local hunting seasons.

In 1977 the Northern Marianas Legislature passed a moratorium on the capturing or taking of fruit bats on all islands (Public Law [P.L.] 5–21, September 1977). The action was prompted by severe declines in fruit bat numbers (largely from commercial hunting), recommendations made by GAWR, and a concern that if local laws were not enacted to protect bats, the U.S. government may step in to regulate them. The moratorium was established for 1 year on islands north of Saipan and for 2 years on the southern islands of Rota, Aguijan, Tinian, and Saipan. The ban on fruit bat hunting has been reauthorized continuously from 1977 to the present.

From 1977 to 1981 there was no agency responsible for enforcing P. L. 5–21 wildlife regulations. In 1981 the newly created DFW was given law enforcement duties. In 1982 two conservation officers (CO's) were hired. As of 1990, DFW employs four CO's on Saipan and three CO's on Tinian. For a short period there was a CO assigned to Rota (D. Stinson, personal communication).

From the beginning, enforcement efforts have been difficult. CNMI law prohibits CO's from carrying firearms in the performance of their duties, some of which are potentially dangerous. CO's have not received special training in law enforcement, and their operations budgets are inadequate; enforcement is not funded by Pittman–Robertson money (Wiles et al. 1989). Hunting and fishing regulations do not have a strong legal precedent in the CNMI, and legal council is reluctant to test them in court. In addition, many politicians do not like unpopular wildlife laws enforced.

There have been a handful of poaching investigations but no convictions regarding fruit bat regulations (Glass and Taisacan, unpublished report). These factors plus poor relations with other CNMI law enforcement officers have created low morale and a poor public image for DFW CO's. It is difficult for CO's to overcome these handicaps.

Commercial Hunting

Commercial hunting of fruit bats in the CNMI began in the mid to late 1960's, peaked in the mid to late 1970's, and continues at a low level today (D. Aldan, personal communication). Commercial trade provides bats for Chamorros living in the CNMI and on Guam. Guam (population 120,000) is the center of fruit bat trade because of its large, relatively affluent Chamorro population and regular airline service. Fruit bat commerce became feasible when incomes allowed families to buy bats, an adequate transportation system became available, and enough hunters were employed to supply large numbers of bats, usually from remote areas. Another factor was the exploitation of bats

on Guam. When native bats became scarce on Guam, a lucrative market for imported bats was created.

The first recorded shipments of bats to Guam occurred in 1970. Complete import records were first compiled in 1975 (Wiles and Payne 1986). From 1975 to 1981 (excluding 1977) about 15,805 fruit bats were shipped to Guam from the CNMI. Rota and Saipan were listed as major suppliers, providing 400–1,900 bats per year from each island (Wiles and Payne 1986). When Guam listed *P. mariannus* as endangered, in 1981, it became illegal to import this species from the CNMI. In 1982 the fruit bat trade from the CNMI to Guam turned into a smuggling operation, for which no data are available.

During boom years entrepreneurs from Guam and Saipan provided local residents with guns, ammunition, and financial incentive to kill as many bats as possible (D. Aldan, personal communication). In some cases gas-powered generators and coolers were provided to store bats on remote islands. Boats and planes made regular pickups in the CNMI. Consumer prices paid for bats fluctuated with supply, ability to pay, and risks taken to acquire them. Initially, prices were in the \$5–10 range, but \$20–25 per bat might be paid by affluent customers on Guam (Brunner and Pratt 1979; D. Aldan, personal communication). Live bats may sell for \$50–100 each.

The negative effects of commercial hunting on CNMI bat populations have been expressed by numerous authors (Wheeler and Aguon 1978; Brunner and Pratt 1979; Ralph and Sakai 1979; Wheeler 1980; Payne 1986; Wiles and Payne 1986). History of wildlife declines worldwide indicates that unregulated harvest of valuable commercial species often threatens species' survival (Greenway 1958).

Special Hunts

Since the 1977 moratorium on taking fruit bats several fruit bat hunting seasons have occurred on Rota. The resource law (P.L. 5-21) included an exemption that allowed the DNR Director to permit special fruit bat hunts with specific dates and harvest quotas. Special seasons requested by the Mayor of Rota have usually coincided with the festival of San Francisco de Borja, the patron saint of Rota. Seasons were 1–4 weeks long with quotas of 15–50 bats, sometimes for designated hunters only.

Experience proved that special season privileges were abused on Rota. Hunting occurred without regard to season dates or bag limits (Lemke, unpublished report; Schmitt, unpublished report). Despite DFW advice not to allow special seasons, political pressure forced the DNR director to authorize a special hunt in 1985 after it had been denied (Schmitt, unpublished report). In 1987, after considerable effort, P.L. 5-21 was amended to eliminate the mechanism for legalizing fruit bat hunts.

In 1988 the DFW experimented with its first limited quota fruit bat hunt on Anatahan, a remote northern island (D. Stinson, personal communication). The 10-day season was open to a small number of hunters on a first-come basis with a season limit of 30 bats per hunter. The hunt was monitored in the field by DFW personnel. The result was a harvest of about 120 bats from a minimum island population of 3,000 bats. The hunt was considered a success in terms of logistics, enforcement, and public acceptance.

Endangered Species Status

The CNMI does not have a mechanism for designating local endangered species. In 1981 Guam listed *P. mariannus* as endangered under Guam statutes, because of declining bat populations and continued illegal hunting. In 1978 Guam petitioned the Service to list Guam fruit bats as endangered (U.S. Fish and Wildlife Service 1978). Six years later the Guam population of *P. mariannus* was listed as endangered under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1984).

In 1986 a petition to list *P. mariannus* as endangered in the CNMI was submitted to the Service (U.S. Fish and Wildlife Service 1987). In review of the petition the DFW recommended that bats on Rota, Aguijan, Tinian, and Saipan be placed on the Federal List of Endangered Species (Schmitt, unpublished report). Since 1986, the DFW has recommended that only bat populations on Aguijan, Tinian, and Saipan be federally listed (Glass and Villagomez, unpublished report; Glass and Taisacan, unpublished report). In 1988 the Service determined that endangered species status for *P. mariannus* populations on Aguijan, Tinian, and Saipan was warranted but precluded by other listing priorities (U.S. Fish and Wildlife Service 1988). Presumably, federal protection on these islands will occur in the future.

In 1989 *P. mariannus* was included with six other *Pteropus* spp. on Appendix I of the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES). Interna-

tional trade is prohibited for species on Appendix I. The CNMI is a participant in the treaty, owing to U.S. affiliation. When enforced, this change in CITES will have a dramatic effect on the commercial fruit bat trade in the Pacific.

Sanctuaries and Wildlife Management Areas

Fruit bat habitat has been protected in the CNMI by establishing Commonwealth Sanctuaries (entire islands) and smaller reserves known as Commonwealth Wildlife Areas. The islands of Maug (1977) and Guguan (1985) have been designated as biological sanctuaries for the protection of fish and wildlife resources (P.L. 5-21). In 1984 the CNMI Public Land Corporation approved the creation of four Commonwealth Wildlife Areas on Saipan (Lemke, unpublished report). Since then, one additional area has been designated on Saipan, and two other areas have been proposed on Rota and Tinian (Villagomez, unpublished report 1987). On small islands, land is highly sought by developers. Sanctuaries and wildlife areas were created to protect remaining wildlife habitat, provide public hunting, and develop methods of habitat improvement.

Conservation Education

The need for an active conservation education program regarding fruit bats in the CNMI has been expressed in several unpublished reports (Lemke, Schmitt, and Glass and Villagomez) and publications (Wiles et al. 1989). The concepts of conservation and wildlife management are foreign to and misunderstood by most residents. In order to achieve long-term goals, future generations of Chamorros must develop a new value system regarding natural resources.

In 1983, the DFW initiated a weekly wildlife column in the Marianas Variety newspaper, which continues to the present (Lemke, unpublished report). Numerous educational articles on fruit bat biology and conservation have appeared. DFW personnel have sporadically presented conservation-oriented slide shows in the public schools. In 1987, DFW produced an educational poster entitled "Let Your Children See the Fanihi!"

Educational efforts have been minimal owing to a lack of priority, funds, and manpower. There are opportunities to develop excellent programs with the help of the CNMI Department of Education and the Northern Marianas College. Conservation education is part of the program that is still deficient.

Discussion

Maintaining and reestablishing fruit bat populations throughout the CNMI is a complex task. Success depends on addressing and resolving difficult political, biological, and social concerns. The following issues are among the most important:

1. *CNMI Politics.* The role of the DFW in charting the direction of resource management has been disputed and challenged since the agency was created in 1981. There is resistance to DFW authority from within the central government on Saipan and from the municipal governments on Tinian and Rota. The DFW needs strong support from the Commonwealth government on major issues and also needs to improve working relations with Rota and Tinian. Agency credibility must be improved at both levels.
2. *Endangered Species status.* The question of the status of fruit bats on Rota needs to be resolved. The Service has been reluctant to reevaluate its decision not to list the Rota population as threatened or endangered because of political ramifications in the CNMI. There is increasing evidence from the DFW that poaching continues to remove a significant number of the bats annually. Poaching and the effects of a typhoon have recently reduced the Rota bat population by over 50% (D. Stinson and P. Glass, personal communication). If the best and most recent evidence points to a biological reason for listing the population, the Service should be willing to make that professional decision.
3. *Biological Information.* DFW has considerable information on fruit bats, particularly on Rota. Most management needs can be addressed with these data; however, there are two areas that deserve more attention. In 1983–84, DFW and others conducted the first bat survey of the northern islands. Since then, bat observations have been incidental to other work. Considering that over 80% of the bats in the Marianas (including Guam) inhabit these islands, the area should be resurveyed every 3–4 years. One goal should be a standardized survey method for each island.

   The recovery or augmentation of fruit bat populations on Aguijan, Tinian, and Saipan should be addressed. It is time to test the biological,

social, and political feasibility of returning bats to Saipan. DFW could capture bats from the northern islands and release them instrumented with radios (preferably with mortality transmitters) in suitable habitat on Saipan. Monitoring of 10–15 bats would answer many important biological and social questions about reintroduction, habitat use, behavior, and mortality. A well-publicized project could have valuable public relations benefits. The impact of illegal hunting could be monitored. Augmentation may be an alternative to natural emigration, which seems slow at best considering distance to viable bat populations.

4. *Enforcement Capabilities*. DFW's enforcement program is in trouble for political and financial reasons. To overcome such obstacles, the enforcement program needs better funding and new leadership. Through no fault of their own, DFW CO's do not have the training or experience needed to perform their duties. DFW could provide new direction by employing an experienced professional CO or Game Warden as a section supervisor. Wildlife enforcement work should be recognized as a specialized profession (like wildlife or fisheries biology) for which local residents have not had the opportunity to train. Hiring a chief CO from the outside on a contract basis (similar to biologists) can provide new leadership, an opportunity to field-train resident CO's, and a fresh professional approach to enforcement. Additional CNMI, CRM, federal, or private conservation funding should be pursued. Other needed changes include permitting CO's to carry weapons and stationing an effective CO on Rota.
5. *Conservation Education*. At present DFW is not set-up to conduct an effective conservation education program even though education is as important as research and management. It would be beneficial to have a full- or part-time position devoted strictly to public education. The position would best be filled by a motivated local resident who could work well with teachers. Additional Pittman-Robertson or private conservation funding could be obtained if aggressively sought after.
6. *Social Alternatives*. Maintaining a total ban on the harvest of fruit bats is not a desirable management strategy for the CNMI. The approach is destined to fail because fruit bats are a highly sought after and culturally significant species. Local residents will only participate in fruit bat conservation if they can see short- and long-term benefits for themselves and the resource. Constant negative reinforcement offers little incentive for people to obey existing regulations. Regulated limited-entry or limited-harvest bat hunts should be pursued; the northern islands of Anatahan, Pagan, and Agrihan offer possibilities. Rota should immediately regulate fruit bat hunting. DFW will be in a better position when it controls the distribution and size of the fruit bat harvest.

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Fruit Bat Population and Conservation Status in the Philippines

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Fruit Bat Population and Conservation Status in the Philippines

In the Philippine Island System of 7,100 islands and islets, Corbett and Hill (1980) listed 34 genera and 80 species of mammals, of which about 40 species are endemic. Fruit bats are well represented in the archipelago (Heaney and Heideman 1987); there are about 23 species, of which 15 (65%) are native. Corbett and Hill (1980), however, listed 32 species of 15 genera, of which 5 genera and 24 species (75%) are endemic. These fruit bats range in size from one of the world's smallest, *Haplonycteris fischeri* (16 g), to the world's largest, *Acerodon jubatus* (1,100 g).

Although precise information on the current population status of many of the native species of Philippine bats is lacking, there is no doubt that threats are accelerating. The principal threat to populations of these species is habitat destruction, which is exacerbated by illegal hunting and the highly restricted ranges of many species. The International Union for the Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Animals (1988) includes 2 (*Dobsonia chapmani* and *Acerodon lucifer*) out of the 10 listed endemic fruit bats as extinct.

The need exists for immediate conservation input and programs for bat species, and the Department of Environment and Natural Resources (DENR) is hopeful that it can better address this problem through collaborative efforts like this conference.

Conservation Measures

In 1988, the Philippino government agreed to give total protection to all wildlife species by initiating institutional reforms and legislative measures. Albeit, this scheme is not entirely considered a panacea to the problems besetting the bat populations, state biologists and policy makers are convinced this initial action is a giant step towards the global quest for species conservation.

Institutional Reforms

The reorganization of the DENR facilitated a renewed call for environmentalism in the Philippines. The reorganization was a response to the opinions of conservationists for a stronger program on wildlife and parks management and, hence, the Protected Areas and Wildlife Bureau (PAWB) was created. The reorganization decentralized the functions of the bureaucracy, providing opportunity for direct management of field resources.

The PAWB is a staff bureau organized to formulate policies and legislation to better address wildlife and parks issues and concerns on a national scale. It is also expected to uphold the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) policies through a CITES management staff.

The bureau is performing at a relatively fast but sure pace, considering the various limiting factors such as low financial support and only fair technical ability of wildlife technicians.

There are still problems in the organization. What matters, however, is the institutionalization

of planning for a better approach to Wildlife and Parks Management.

Policy Reforms

Between 1988 and 1989, the bureau implemented two important policies that brought about radical changes in the direction of the use, harvest, and trade of wildlife.

1. *DENR Administrative Order (AO) 90, Series of 1988.*

This AO established a national quota for specific wildlife that may be collected from the wild for trade purposes. All species of bats were excluded from the quota, totally banning trade of the species, even locally.

In 1989, we received applications for about 5,000 fruit bats for exportation to Guam, but rejected them because of this policy. Note, the absence of a quota automatically declares that collection from the wild is illegal and, hence, even inter-island transport is prohibited.

2. *DENR Administrative Order 96, Series of 1988.*

This AO establishes the policy of a gradual phase-out in the collection and exportation of fauna from the wild. The schedule for reduction and total phase-out is as follows:

a. avian species—10% reduction of the national quota (NQ) starting in 1990 until final phase-out in 1994,
b. mammals—20% reduction of the 1989 NQ until final phase-out in 1994,
c. herptiles—10% reduction of the 1989 NQ until final phase-out in 1994, and
d. invertebrates—15% reduction of the 1989 NQ until final phase-out in 1994.

This AO also creates an Interagency Wildlife Management Committee composed of members from academia, nongovernment organizations, the exporters group, and the DENR. This scheme reduces the chance of a biased decision in the allocation and distribution of wildlife quotas among qualified applicants. It also provides a partial solution to the meddling of influential persons in the decision-making process by virtue of the technical and independent nature of each member.

Another salient feature of this AO is the requirement of installing a marking system for wildlife, such as tattooing for mammals (a process is used with monkeys) and banding for birds.

International Commitment

The PAWB, as the Philippine Management Authority for CITES matters, renewed its commitment to CITES during the conference of the parties held on 20 October 1989, in Laussane, Switzerland. The Philippine delegation unanimously voted for the proposals concerning the protection of fruit bats. We are continuously exploring the possibility of cooperative projects that would ensure the adoption of specific projects, particularly on fruit bats.

Site Protection Measures

Limited financial resources at the DENR have prevented an active bat conservation program. Gradually, however, the DENR, through PAWB, is considering means by which field personnel could be trained to set future plans directed to specific projects. The DENR, World Wildlife Fund, and Haribon Foundation, a local NGO, under the Debt-for-Nature Swap Program, are training technicians in wildlife management. For 1990–91, regional technicians are slated for 240 h of training.

Conclusion

There is still a bright future for flying foxes in the Philippines, though active management on a grand scale is necessary. For now, successfully controlling the legal and illegal trade of the species is sufficient.

This workshop was timely, as it paved a new road to explore collaborative efforts for bat conservation. We hope that what remains to be witnessed is the survival of the magnificent flying foxes for eons.

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Fruit Bats in American Samoa: Their Status and Future

by

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Introduction

Two species of fruit bats (flying foxes) appear in American Samoa. *Pteropus samoensis* is solitary and diurnal. *Pteropus tonganus*, the more abundant of the two species, is colonial and crepuscular–nocturnal. These bats have played a role in Samoan culture (Sinavaiana 1992) and are currently hunted for recreation and subsistence. This paper reviews the status of fruit bats in American Samoa, including relevant conservation legislation, population trends, hunting pressure, and other management issues.

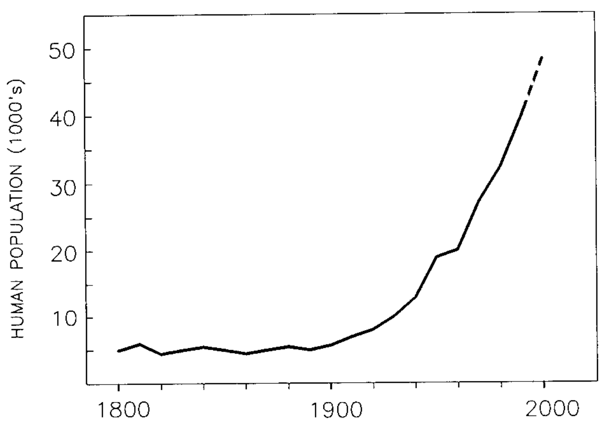

Fig. 1. Human population growth in American Samoa. Source: 1900–2000 (EDPO 1988); pre-1900 was based on scant records.

Study Area

American Samoa, located 4,200 km southwest of Hawaii, consists of five small volcanic islands and two atolls. The largest island, Tutuila, is 142 km^2 and supports nearly 90% of the rapidly expanding human population in the Territory (Fig. 1). The estimated population in 1990 was 46,600 people, increasing at about 3.7% per year.

As elsewhere in the South Pacific, bats are the only indigenous mammals in American Samoa. Fruit bats are found on the five larger islands, which are mountainous and largely covered by rain forest, secondary growth, and agricultural plantations. These islands have steep slopes with limited areas suitable for human settlement and agriculture.

Legislative Protection

Since 1986, it has been illegal to export or commercially hunt fruit bats in American Samoa. Before 1986, annual exports from American Samoa to Guam increased from about 200 bats in the early 1980's to almost 2,000 bats in 1984 (Wiles and Payne 1986).

Legal restrictions by the Samoan government also apply to private or subsistence hunting (although enforcement is lacking): (1) there is a 3-month hunting season, (2) the bag limit is 7 bats per day, (3) shooting at roosts is prohibited,

(4) daytime hunting is prohibited (in order to protect *P. samoensis*), and (5) bats cannot be sold or bartered.

In 1989, Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) listed both *P. samoensis* and *P. tonganus* as species in which international trade is prohibited.

Methods

Methods for determining the relative abundance and hunter harvests of fruit bats are summarized below. Further details are described by Knowles (1989) and Department of Marine and Wildlife Resources (1990).

An index of relative abundance was derived by the use of daytime surveys (Wilson and Engbring 1992). In 1989, 43 bat counts were made at 19 habitat stations at varying times of day and on different days. These stations ranged in size from 0.1 to 2.5 km^2 (average 0.9 km^2) and covered a total of 17 km^2, equaling 12% of the land area of Tutuila Island. Survey locations differed slightly during the 3 years of study (1987–89). At each station, the observer was stationary and viewed a large area of terrain for 20 min during either of two periods (0500–1115 h or 1500–1930 h), because bat activity decreases somewhat during midday, particularly for *P. tonganus*.

Observed bats were classified as either using the study area or merely flying over it. Bats that flew over the ridges or well above the canopy and did not stop in the study area were assumed to be only flying over and were not included in the estimate of relative abundance. Bats observed eating, resting, or flying within or just above the forest canopy in the area were assumed to be using it. Given that it was possible to record the same bat on more than one occasion, the observer provided a final best estimate of the number of individual bats using the study area during the observation period. The relative abundance index was then calculated as the total number of individual bats using all study sites during all surveys divided by the total number of surveys conducted. Wilson and Engbring (1992) discussed a number of possible biases inherent in this method of estimating relative abundance.

A preliminary estimate of the hunter harvest was obtained by interviewing a subsample of subsistence hunters on Tutuila Island. In 20 of the possible 60 villages, 60–90 hunters were interviewed every 3 months from April 1990 to March 1991. The islandwide harvest was estimated from the sample interviews for all hunters on the island. The latter was calculated by assuming that the ratio of hunters to people in the sampled villages was similar to the ratio of all hunters to all people on the island. Numbers of the two species of fruit bats killed were combined because many hunters do not differentiate between the two species. Because of potential sources of bias in the interview process, such as recall inaccuracy or the purposefully inaccurate reporting for fear of legal consequences, we believe the interviews yielded only a general picture of annual harvest levels.

Results

Population Trends

The abundance of the Samoan fruit bat (*P. samoensis*) on Tutuila Island has varied since systematic surveys began in 1987 (Fig. 2). The largest change between survey periods occurred during a single month (December 1987–January 1988) when the index fell by one half. It seems unlikely that this large change in the index accurately reflects a population change; the index change more likely reflects the impreciseness of the index to track population levels. If this is so, the increase in the index during the last observation period (April–May 1989) does not necessarily represent an increase in bat numbers.

For the Tongan fruit bat (*P. tonganus*), a population increase may be occurring on Tutuila Island (Fig. 2). The abundance index shows a persistent increase since 1987.

Subsistence Hunting

At present, approximately 1% of the American Samoa population hunts. Fruit bats are hunted year-round for two reasons—the hunters are unaware of existing regulations that limit legal hunting to 3 months, and the regulations are not enforced.

An estimate of the number of fruit bats killed annually by hunters is complicated by a special event that occurred during the study period—Hurricane Ofa (February 1990)—which dramatically increased the bat harvest. After the hurricane, bats were exceptionally vulnerable to human harvest (see Discussion); thus the estimated harvest (2,800 bats) during the months following the hurricane (Table) is probably not indicative of typical hunting pressures.

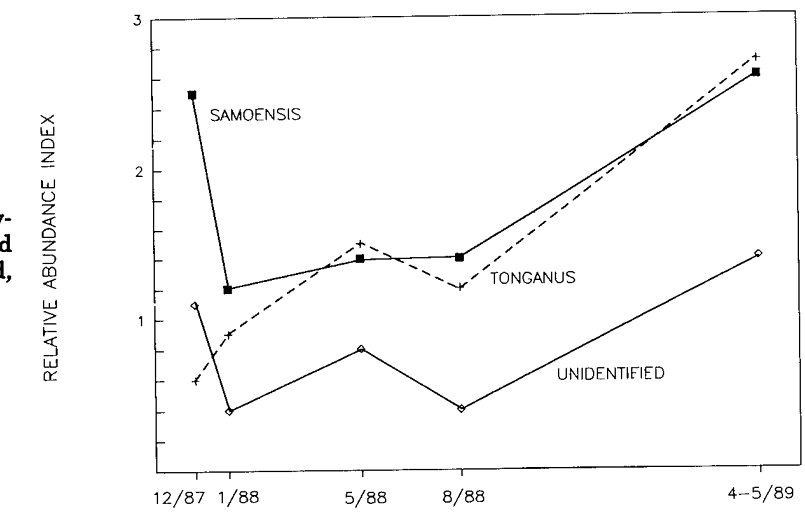

Fig. 2. Relative abundance index for daytime-active fruit bats in combined habitat stations on Tutuila Island, 1987–89.

The high numbers of bats taken during the next 3½-month-period (July–October 15) may also have been influenced by the hurricane's effects or may realistically reflect an increased hunting pressure before a major holiday in American Samoa (White Sunday in early October), when hunting, especially for birds, is a well-known event.

Consequently, we have estimated the total harvest in two ways. The lower estimate assumes that only the last two quarters sampled reflect typical year-round hunting pressures; the high estimate assumes the same except for the one quarter which had increased hunting pressure because, presumably, of the White Sunday holiday. In this manner, we estimate that 700–2,300 fruit bats are probably killed annually by hunters on Tutuila Island.

Table. *Estimate hunter harvest of fruit bats on Tutuila Island, American Samoa, following Hurricane Ofa in February 1990.*

Quarter	Estimated total harvest fruit bats[a]
1. April–June 1990	2,800
2. July–15 October 1990	1,800
3. 15 October–December 1990	130
4. January–March 1991	230
Total	4,960
Modified annual harvest estimate	700–2,300[b]

[a] Includes both *P. samoensis* and *P. tonganus*.
[b] See text for explanation.

Discussion

If our data accurately reflect bat abundance, then population levels of fruit bats have been relatively stable during the past few years, a finding similar to that of Wilson and Engbring (1992). We caution, however, that there are potential pitfalls in the use of daytime counts of fruit bats to monitor their relative abundance. While the method is convenient, daily activity patterns and other factors (e.g., hunger) can affect the numbers of bats active during the daytime, thereby complicating the interpretation of changes in the index. Further field studies are needed to test the reliability of this method.

We do not know how current population levels of bats on Tutuila compare to levels in the past, but anecdotal accounts suggest that former levels were higher. Hunting and habitat degradation because of farming and other human activities may have caused population reductions, and such pressures will presumably increase as the human population grows (Fig. 1).

We speculate that the recent Hurricane Ofa, which hit American Samoa in February 1990, caused significant mortality to fruit bats in two ways. First, the devastation caused by the storm probably killed some bats either directly or by blowing them far out to sea. Second, the surviving bats had difficulty finding food because the storm stripped virtually all fruit off the trees. It is likely that some bats starved in the weeks following the hurricane. An additional indirect effect was that the bats were more vulnerable than usual to hunting as they flew into villages in an apparent search for food.

Such severe weather events are, however, a characteristic feature of the South Pacific region. During the period 1840–1966, six hurricanes (sustained winds over 75 mph) and 42 tropical storms (sustained winds 40–75 mph) hit somewhere in the Samoan islands, for an average of one major storm event every 3 years (U.S. Army Corps of Engineers 1980). Fruit bats are thus almost certain to encounter one or more such storms during their lives because of their potentially long lifespan (up to 17 years—Koopman and Cockrum 1967). Because of this high probability of encounter, the bats may have evolved adaptations to such disturbances. For example, bats may have developed behavioral patterns to improve their short-term survival during such storms, such as roosting in protected areas or near the ground.

Life history traits of a population also provide a strategy to cope with ecological problems commonly encountered by a population (Stearns 1976). For many species, these traits tend to be associated in two general patterns that have been called r-selection and K-selection. Colonizing species are good examples of r-selected populations. They face a high rate of adult mortality each year; to survive over the long run, there must be a high rate of annual recruitment to the population. Individuals in these populations exhibit rapid growth, a short lifespan, and a high annual reproductive effort. In contrast, K-selected species (e.g., redwood trees) have relatively high survival rates of adults but low annual recruitment of young into their population. Adults are thus long-lived and reproduce enough times so that, despite the low recruitment of young, the population survives.

Fruit bats appear to have K-selected traits. Scattered data for several fruit bat species (Falanruw 1988) indicate that females generally have lengthy gestation (4–6 months) and weaning (2.5–6.8 months) periods, and produce one young per year. There is also a prolonged period before the young reach sexual maturity (1.5–2 years). The resulting recruitment rate of fruit bats is extremely low compared with other mammals of similar size. To offset this low recruitment, life expectancy may be long—one captive bat lived 17 years.

While a long life span buffers fruit bat populations against short-term adversity and a low recruitment rate, it also makes them vulnerable to any activity, such as hunting, that targets the adult segment of the population. A significant loss of breeding members, coupled with a low recruitment rate of young, would cause population numbers to be reduced and retard the recovery of the population to former levels.

Summary

Five small islands in American Samoa support populations of the fruit bats *P. samoensis* and *P. tonganus*. Abundance indices indicate that both populations have been relatively stable in recent years (1987–89) despite substantial mortalities from hunting. But continuing habitat alteration because of agriculture, and potentially greater hunting pressure from a rapidly growing human population, pose problems that the bats may be poorly adapted to meet. The slow reproductive rate and longevity of adults, though a seemingly successful strategy for meeting recurring natural disasters such as hurricanes, may be less successful in accommodating increases in hunting pressure and other human-caused effects.

Acknowledgments

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Protection of Flying Foxes on Yap Islands

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Introduction

Yap State in the Western Carolines provides an example of successful conservation of flying foxes. The process, however, has not been without challenges. We describe some of the ecological, biological, and social factors relevant to fruit bat management, and the experiences of one island state that has made an effort to protect this special resource.

Flying Fox Habitat

Yap seems to offer ideal habitat for fruit bats. Much of the coast is ringed by mangroves, which make up about 12% of the vegetation. Inland of the mangroves, people have developed tree garden agroforests. As of 1974, these agroforests covered some 27% of Yap. Inland of the agroforests there is a mosaic of forest and secondary vegetation resulting from the shifting agricultural activities of people. These areas compose about 28% of the land area. About 22% of the island is covered with savanna lands (Falanruw et al. 1987). The vegetation of the atoll of Ulithi is largely strand, atoll forest, agroforest, and a bit of mangrove in the interior of one or possibly two islets of the atoll. Mangroves and forest areas provide both food resources and suitable roosting areas. Agroforests are rich in food resources, and flight paths between roosting areas and agroforests are commonly observed. Fruit bats also feed on *Pandanus*, which is common in savanna areas.

The traditional lifestyle of the Yapese, combined with private ownership of almost all land and limited finances, has limited the conversion of large areas of land from the vegetation types described above. Thus, Yap seems to provide a similar habitat for fruit bats today, as it has for the past three generations. Until this changes, there is optimal opportunity for people to learn to manage this resource. If people can learn to conserve fruit bats, there is potential for wisely using other resources as well.

Biological Factors

A U.S. Forest Service study of fruit bats from 1979 to 1981 (Falanruw, unpublished manuscript, and 1988b; Morse et al. 1987) revealed several factors relevant to the management of these animals. First, although literature over the last 54 years has described definite breeding seasons for bats of the genus *Pteropus*, the Yap population produced young throughout the year. Second, observations and measurements of a large number of fruit bats from Yap and Ulithi show that there is considerable overlap in the characteristics used to distinguish among *Pteropus* from Guam, Yap, and Ulithi (Falanruw 1988b, 1989).

Traditional Utilization of Flying Foxes

In the past, when Yap's human population was high, the use of natural resources was culturally regulated (Falanruw 1982). Flying foxes were not an esteemed food and were eaten mainly by less powerful groups who lived inland and had limited or no access to marine resources. Harvesting of fruit bats was largely done with nets. Flight patterns of fruit bats were observed and platforms erected near feeding trees. Bats were then netted in the evening when they came to feed (Falanruw 1988a).

The human population of Yap declined considerably from the time of outside contact until the end of the period of Japanese occupation (Useem 1946). As the population began to rise during the American administration of the islands, new food resources became available, and old cultural patterns began to break down. By 1965, fruit bats were commonly observed flying into savanna habitat at dusk and returning to roosting areas at dawn.

The Flying Fox Trade

While consumption of bats on Yap is limited, fruit bats are sought after as a specialty of the Chamorro cuisine on Guam, Saipan, and Rota. After the decline of fruit bat populations and the imposition of hunting restrictions on Guam, Chamorros on Yap began to export bats to Guam. As Yap became known as a new source of fruit bats, exploitation patterns changed. The monetary value of the resource increased at a time when the road system was being expanded. This gave the general public greater access to the resource. Individuals who were not the traditional users of the resource, as well as non-Yapese, began exporting fruit bats.

Management Efforts

In 1975, the Yap Legislature passed a law limiting the hunting of fruit bats to October through December. This law was ignored, and export records show more bats were exported during the closed season than during the open season. The number of bats known to have been exported from Yap increased from a few in 1974 to over 7,288 in 1980 (Falanruw 1988b). The actual number killed was even greater, and many shipments of bats went unrecorded as bats became an even more valuable commodity than fish for people travelling to the Marianas.

With the development of the fruit bat trade, the number of guns, largely .22's and shotguns, on Yap increased considerably beginning in 1975. By 1977, the ratio of bats exported to the number of registered guns dropped markedly; however, the total number of bats exported increased. By 1979, bats were becoming harder to hunt in savanna areas, and several prominent local hunters withdrew from the trade. By 1980 and the early months of 1981, however, the business became more commercialized, and bats were shot largely in their roosts. Data collected from air freight records in 1980 showed that about 70% of flying fox exports involved foreign businessmen. This information and preliminary data from the U.S. Forest Service study of fruit bats (Falanruw, unpublished manuscript) were presented to the Yap Legislature. In May 1981, fruit bats were protected throughout the year and accompanying legislation outlawed the private use of guns on Yap. The decrease in the number of firearms and enforcement of Yap's regulations by Guam custom officers brought an end to the major trade in fruit bats. Incidental hunting for local consumption continued. With the end of the export trade, fruit bat populations increased from an estimated 1,000–2,000 in 1981 to an estimated 5,000 by 1986 (Engbring, unpublished manuscript).

The flying foxes of Ulithi, described in 1932, seem to have been relatively inconspicuous, leading local residents to report that fruit bats came to

Ulithi after typhoon Ophelia in 1960. Previous patterns of cultural use are not known, but the animal, whose original Ulithian name has been popularly changed to one meaning "rat of the air," is seldom eaten in Ulithi. A 1986 census of the fruit bats of Ulithi (Wiles et al. 1991) estimated 1,200 animals for the 4.5 km^2 of land on scattered islets of the atoll. Observations of feeding patterns and the local flora suggest that the population was near carrying capacity.

Desire to hunt bats increased after typhoons in 1986 and 1987 damaged the vegetation and breadfruit crop of Ulithi, and bats became more conspicuous. At the same time, people were becoming aware that increasing numbers of bats were being illegally exported to the Marianas. Between 1986 and 1989, Commonwealth of the Northern Marianas Islands (CNMI) fruit bat import records show that at least 2,101 bats were imported from Yap. Concern over the unfairness of poaching activities on mainland Yap, and requests from Ulithi, led the Yap Legislature to consider a bill to establish a hunting season and issue firearms during the hunting season. After a public hearing on the matter, the legislature amended the 1981 law prohibiting the taking of fruit bats to provide for hunting during November, when declared by the Governor of Yap. The Governor's declaration could identify the areas or islands within the state where hunting may or may not take place. The prohibition on private ownership of firearms, other than airguns, was maintained.

Despite the ban on firearms, a 1-month hunting season for fruit bats was declared in November 1988, limited to fruit bats from Ulithi. Exports of bats from Yap State to Guam continued beyond the period of this open season until it was announced that bats could not be exported after the declared season. In response to the concern over the unfairness of poaching activities, the state began to prosecute persons apprehended for illegally harvesting bats (Yinug et al. 1989). To date, three parties have been convicted and fined for illegal commerce in bats. A fourth case is still before the court because of a challenge to the existing law.

Discussion

Cessation of major exports of fruit bats from Yap, for 5 years, resulted in a reversal of the population decline, in spite of some harvest for local consumption throughout this time. The repeated incidence of illegal export activity shows, however, that continued vigilance in enforcing laws is needed. Geist (1987) provided historical evidence that a market value on dead specimens of vulnerable wildlife generates an infrastructure that attracts illegal activity, and protecting such wildlife from poaching is costly. The island states of Micronesia do not have the financial base to support such surveillance and enforcement efforts. The placing of *Pteropus mariannus* on Appendix I of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) should be effective in abating commercial exploitation of Yap's bats, if regulations prohibiting imports into the U.S. Territory of Guam and Commonwealth of the Northern Marianas are enforced and transhipment is controlled. History teaches, however, that when the public is alienated from the management of wildlife resources they lose interest or exterminate wildlife when outside control slackens (Geist 1987). This is especially possible on widely separated small islands. Therefore, it is important that international regulation of trade in fruit bats be accompanied by local consciousness-raising about the need for wise management of fruit bats and other resources.

If Yap follows the pattern of other countries trying to develop an island economy to support an American lifestyle, considerable changes in natural habitat can be expected. With a loss of natural habitat, even local use of the fruit bat resource could seriously impact populations. Continued vigilance is needed. The cooperative efforts of the Fish and Wildlife Service personnel from Hawaii with local personnel in conducting population counts and conducting basic studies should be continued in the interest of conserving not only Yap's bats, but also those of Guam, which are more imminently threatened with extinction. A better understanding of the genetic relations of fruit bats from Guam, Ulithi, and Yap could be important to future management strategies as well.

In the area of developing public consciousness and appreciation for Yap's flying foxes, volunteer efforts have been ongoing since 1979, including activities such as visits of pet flying foxes with children of all ages, fruit bat puppets and stories, and features in the Yap almanac calendar (Figs. 1 and 2). Efforts are currently underway to develop a flying fox image similar to Smokey the Bear to serve as a symbol for conservation efforts.

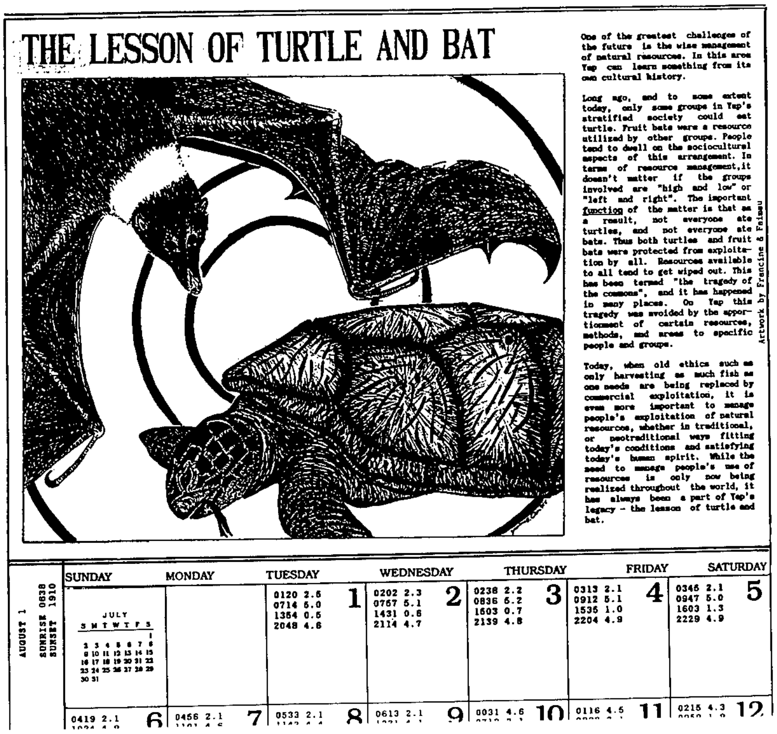

Fig. 1. Illustration from the Yap almanac calendar for 1986.

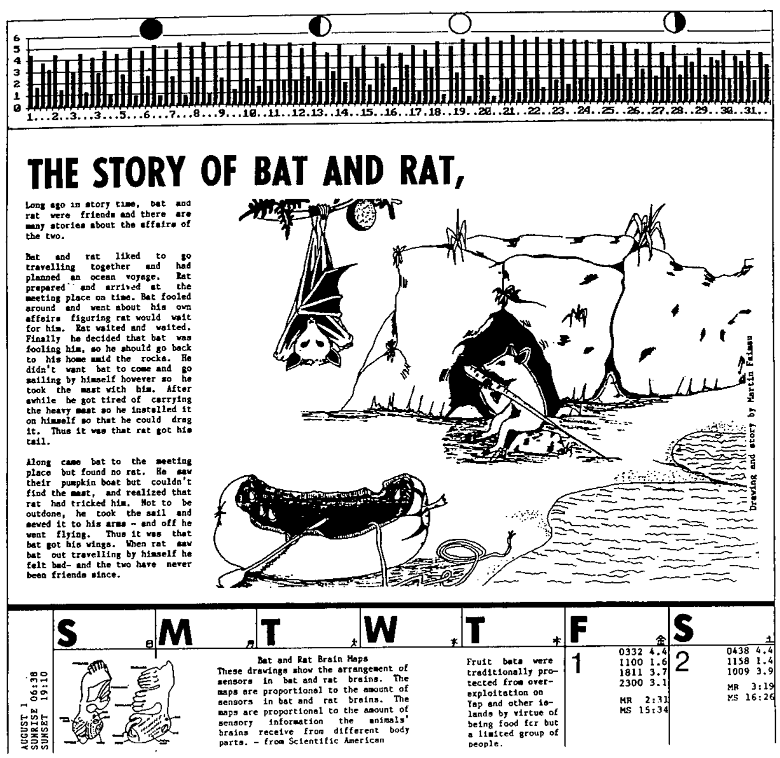

Fig. 2. Illustration from the Yap almanac calendar for 1989.

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Conservation of Pacific Island Flying Foxes and the Convention on International Trade in Endangered Species of Wild Fauna and Flora

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Introduction

Many believe the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) is the most successful of international wildlife conservation instruments. When implemented properly and enforced, the treaty effectively stems overexploitation for international trade. In some instances, the treaty rationalizes overuse, to allow for increased capitalization of populations of certain species. The degree of protection afforded by CITES and the contribution that protection makes to the survival of a particular plant or animal species depend largely on the conservation status and trade potential of that species. Often, complex social and economic factors also play a role.

In the case of flying foxes, the full scope of factors affecting the long-term survival of most wild populations has not been completely documented. Conservation biologists and international policy makers have focused most of their attention on stemming the international trade that has decimated populations on several Pacific islands. The emphasis thus far on the trade aspects of flying fox conservation made this issue a remarkable case study on the limitations of CITES because of inadequate implementation of its provisions by a member government. Failure by the United States to implement and enforce CITES-mandated trade controls has undermined the treaty's effect on the trade of these species and on their conservation. Recent developments within CITES and the United States promise at least partial resolution of this trade problem, at which point other, less clear-cut, economic, and cultural issues are likely to require analysis and attention.

The CITES Infrastructure

CITES was concluded at a plenipotentiary conference in Washington, D.C., in March 1973 and entered into force in July 1975. At present, the treaty counts 112 countries as members, including a number in Oceania—or Australia, New Zealand, Papua New Guinea, the Philippines, and Vanuatu. American Samoa, the Commonwealth of the Northern Mariana Islands (CNMI), Guam, and Palau, as United States jurisdictions to which the U.S. Endangered Species Act applies, also fall under the treaty.

Internationally, CITES is administered by the CITES Secretariat, based in Lausanne, Switzerland, under the auspices of the United Nations Environment Programme. The primary responsibilities of the Secretariat include arranging and servicing meetings of the treaty Parties, both the biennial meetings of the Conference of the Parties and regular meetings of CITES committees; communicating with the Parties on issues of implementation and violations of the treaty; and carrying out duties related to the proper functioning of the treaty.

Implementation and enforcement of CITES are conducted at the national level. When becom-

ing party to the treaty, a government is responsible for designating an agency as Management Authority to carry out various duties assigned to that authority under the terms of the treaty. These duties include issuing permits for trade in species regulated by the treaty, communicating with the CITES Secretariat and other governments, and compiling annual reports of trade in CITES-listed species for distribution. A CITES Party must also designate a Scientific Authority to fulfill specific responsibilities established by the treaty. The role of the Scientific Authority is an important one, as it provides the scientific underpinnings of the treaty in the form of biological findings on which the Management Authority issues permits, monitoring of permits and trade levels and assessment of the impact of trade on species' populations, and advice to the Management Authority as to regulatory measures appropriate for ensuring trade is not detrimental to species' survival.

Customs or similar agencies usually enforce the terms of the treaty. Responsibility includes inspection of CITES shipments, verification of CITES permits, and penalization of treaty violations. In the United States, enforcement of wildlife trade laws is generally the responsibility of the U.S. Fish and Wildlife Service, Division of Law Enforcement. In certain instances, however, such as imports of wild birds and plants, the responsibility is shared with the Animal and Plant Health Inspection Service (APHIS) of the U.S. Department of Agriculture.

CITES Regulations

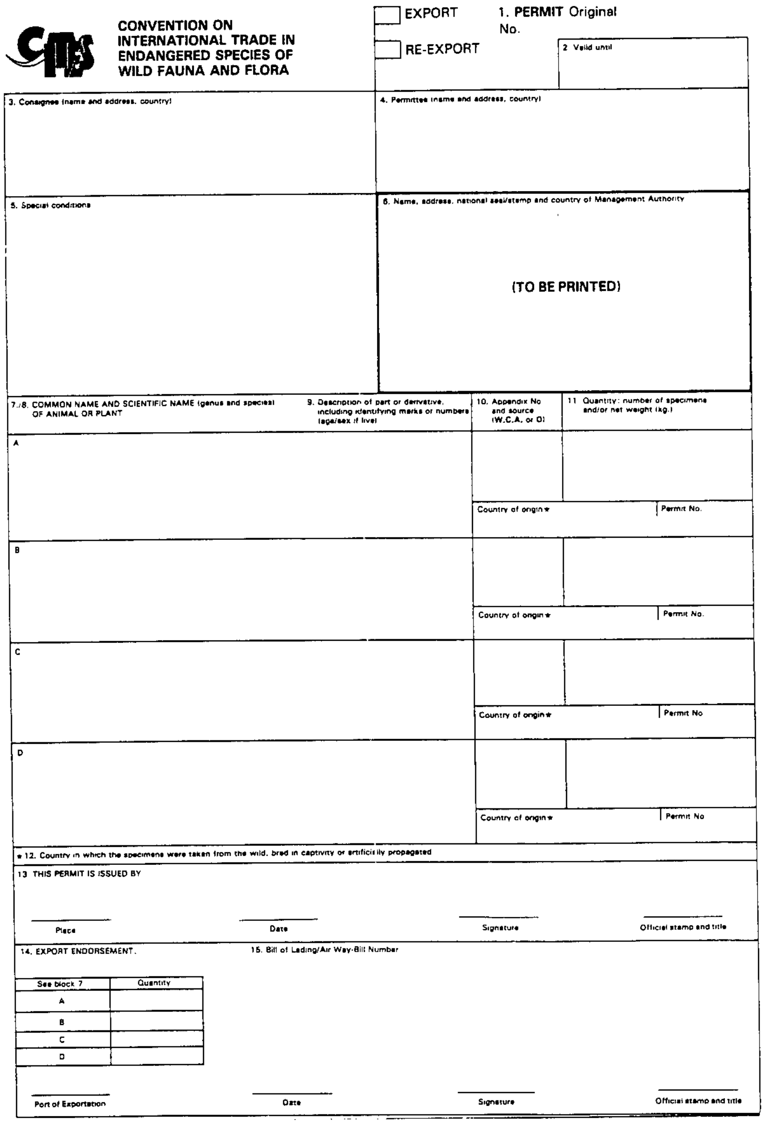
CITES is not an international endangered species list. Its purpose is to ensure international trade does not threaten species' survival. CITES includes among the species it protects common species traded in very high numbers and excludes some of the world's most endangered species based on their absence from and lack of potential for international trade. The treaty functions on the basis of its four appendices, three of which list species to which varying degrees of trade controls are to be applied and the fourth being the permit that is to accompany every international transaction involving a listed species.

As provided for in Article II of the treaty, Appendix I includes species threatened with extinction that are or may be affected by trade and in which trade is only authorized in exceptional circumstances. Appendix II includes species that may not presently be threatened with extinction, but might become threatened if trade is not regulated. Appendix II also lists "look-alike" species, to ensure effective control of trade in listed species to which they bear a close resemblance. Appendix III includes species that are regulated in trade by specific Party members.

For species listed on CITES Appendix I, international trade for primarily commercial purposes is prohibited and may only be allowed on the basis of an import permit issued by the Management Authority of the importing country and an export permit issued by the Management Authority of the exporting country on the basis of the prior-issued import permit. In both the importing and exporting countries, the Management Authority must issue a permit after the Scientific Authority has determined the proposed trade will not be detrimental to the survival of the species. The Management Authority of the exporting country has an additional responsibility—to ensure that the specimens to be exported were not illegally acquired.

International trade in Appendix II species requires issuance of an export permit only by the Management Authority of the exporting country and presentation of that permit before import. An export permit is to be issued only when the Scientific Authority of the exporting country has ruled that the export will not be detrimental to the survival of the species and the Management Authority has determined that the specimens in question were legally acquired.

The Scientific Authority "non-detriment" finding for trade in Appendix I and II species is the keystone of CITES. For this reason, the treaty is very specific in its definition of "detriment" and prescription of measures to be taken by member governments to ensure it does not occur. As elaborated with respect to trade in Appendix II species in Article IV, the Scientific Authority is responsible for determining when export of a given species should be limited "in order to maintain that species throughout its range at a level consistent with its role in the ecosystems in which it occurs." The Scientific Authority must also advise the Management Authority as to suitable measures to be taken to limit the grant of export permits for specimens of that species. However fundamental, the explicit provision for the conservation of the ecological role of species is often ignored by CITES authorities and government policy-makers, and export permits for CITES species are regularly issued independently of a scientific non-detriment finding.


CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES OF WILD FAUNA AND FLORA

EXPORT
RE-EXPORT

1. PERMIT No. Original

2. Valid until

3. Consignee (name and address, country)

4. Permittee (name and address, country)

5. Special conditions

6. Name, address, national seal/stamp and country of Management Authority

(TO BE PRINTED)

7./8. COMMON NAME AND SCIENTIFIC NAME (genus and species) OF ANIMAL OR PLANT	9. Description of part or derivative, including identifying marks or numbers (age/sex if live)	10. Appendix No and source (W,C,A, or O)	11. Quantity: number of specimens and/or net weight (kg.)
A			
		Country of origin *	Permit No.
B			
		Country of origin *	Permit No.
C			
		Country of origin *	Permit No.
D			
		Country of origin *	Permit No.

* 12. Country in which the specimens were taken from the wild, bred in captivity or artificially propagated

13. THIS PERMIT IS ISSUED BY

Place | Date | Signature | Official stamp and title

14. EXPORT ENDORSEMENT:

15. Bill of Lading/Air Way-Bill Number

See block 7	Quantity
A	
B	
C	
D	

Port of Exportation | Date | Signature | Official stamp and title

Figure. Permit form adopted by the Parties in 1981.

Frequent departure by CITES member governments from these very specific procedures has considerably compromised the effectiveness of the treaty and, in turn, the conservation prospects of many heavily traded species.

Additional requirements for the issuance of CITES permits are set forth in Article VI of the treaty and several of the resolutions adopted by the Parties since 1975. The model permit form adopted by the Parties in 1981, through Resolution Conference 3.6 (Figure), revised the permit information requirements as established in Appendix IV, while a system of numbered security stamps individualized by country for validating permits has since been instituted. Other requirements are that a separate permit accompany each consignment of CITES specimens, that a permit be valid for only 6 months from the date of issue, and that permits not be issued retroactively.

While providing for the exercise of control over individual shipments, CITES permits also provide a basis for trade-monitoring based on annual reports of trade in CITES-listed species. Compiled data from CITES permits enables global assessments of trade levels in particular species and comparison of data from both importing and exporting points. The latter analysis provides a basis for assessing the effectiveness of trade controls at both ends.

In cases of trade in CITES specimens with a country not party to CITES, Article X provides for the acceptance by CITES Parties of "comparable documentation" issued by the appropriate agency of a nonparty state that substantially conforms

with the requirements of the treaty for permits and certificates. There seems to be ample basis for interpreting this requirement as including a scientific non-detriment finding on the part of a non-party state, although it is clear that very few, if any, CITES Parties do so.

Amending the CITES Appendixes to Include Flying Foxes

Species are added to or deleted from the CITES Appendixes through procedures established in the treaty. Amendments to Appendixes I and II are approved by two-thirds vote at the biennial meetings of the treaty Parties or through vote by postal procedure, whereas Appendix III is amended simply through notification of the CITES Secretariat of the species to be listed. The Parties have adopted specific scientific and informational requirements that must be applied to proposals to amend Appendixes I and II. These requirements include conclusive data documenting trends in species' populations and levels of domestic use and international trade.

In 1987, the CITES Parties approved, for the first time, protection of flying foxes through the inclusion of nine species of the genus *Pteropus* (Table), including two believed to be extinct, on CITES Appendix II. Instead of providing a basis for the control of shipments and stimulus to exporting countries to manage populations of these species, the Appendix II listing served little apparent purpose, mainly because the United States authorities, at the importing end, failed to institute CITES trade controls. The absence of federal wildlife personnel on Guam and in the CNMI precluded the application of such controls to the 40,000 flying foxes imported into those two jurisdictions in 1988 and 1989 (Brautigam and Elmqvist 1990; D. Stinson, personal communication).

The devastating effects of continued uncontrolled trade of flying foxes into the United States subsequent to the CITES Appendix II listing prompted the governments of the United States and Sweden to propose increased CITES protection for flying foxes, in 1989. As a result of these two proposals, seven of the *Pteropus* species listed on Appendix II in 1987 were transferred to Appendix I (Table), and the remaining unlisted species of the genus *Pteropus* and six species of the genus *Acerodon* were included in CITES Appendix II.

Table. *Listing of flying foxes on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendixes.*

Species name	Appendix I	Appendix II
Acerodon spp.		1989
Pteropus spp.		1989
Pteropus insularis	1989	1987
Pteropus macrotis		1987
Pteropus mariannus	1989	1987
Pteropus molossinus	1989	1987
Pteropus phaeocephalus	1989	1987
Pteropus pilosus	1989	1987
Pteropus samoensis	1989	1987
Pteropus tokudae		1987
Pteropus tonganus	1989	1987

Although the Appendix II listings were primarily for look-alike reasons, several of these species are believed to be threatened with extinction.

In practical terms, the recent CITES Appendix I listing provides for a prohibition on international trade in those species occurring on the islands of the central and western Pacific, while the Appendix II listing provides for regulation of international shipments containing all other *Pteropus* and *Acerodon* species. As required by the treaty, any international transactions in the Appendix I flying fox species must be permitted by the Management Authority or appropriate agency of both the importing and exporting country on the basis of scientific findings by the scientific authorities in both countries. In order to be accepted for import by a CITES Party, such as the United States, international shipments of Appendix II flying foxes require presentation before import of a CITES export permit or comparable documentation issued by the Management Authority or appropriate agency of the exporting country.

Like most legal instruments, CITES provides for exemptions to certain requirements under certain circumstances. Article VII of the treaty establishes exemptions for species listed in Appendix I in cases where specimens are captive-bred or were acquired before the treaty entered into effect for them, are traded for purposes of scientific loan or exchange, or are personal and household effects. The treaty is very specific with respect to what constitutes personal and household effects and clearly prohibits the import of specimens of an Appendix I species acquired by a person outside his usual country of residence into that country. In the United States, the law is equally strict and

prohibits import by U.S. residents of Appendix I wild plants and animals that were acquired outside of the United States. It is, therefore, clear that no Appendix I flying foxes may legally enter the United States for either commercial or personal purposes.

Because CITES governs only international trade and not domestic use, the recent Appendix I listing risks increasing pressure on those taxa occurring within U.S. territory on Guam, in the CNMI, and Palau. Local legislation prohibiting hunting and trade of *P. mariannus* populations on Guam and in the CNMI and the listing of the Guam population of *P. mariannus mariannus* under the U.S. Endangered Species Act should provide sufficient protection for these populations, given active enforcement by wildlife officials. However, past levels of trade and the apparent lack of controls on hunting and trade point to potentially serious overexploitation of the subspecies *P. mariannus pelewensis* in Palau. This problem requires immediate attention.

Conclusion

Based on a review of its provisions, CITES would seem to offer sufficient safeguards to ensure that international trade does not threaten species' survival. An increasingly sophisticated permitting system, a dual-permit requirement for trade in Appendix I species, scientific findings for transactions in listed species, and other elements point to such a mechanism. However, CITES is only as effective as its implementation and enforcement by its member governments, and the trade in flying foxes has been a particularly compelling example of CITES' limitations because of shortcomings in implementation at the national level. The United States did not fulfill fundamental responsibilities governing trade in CITES Appendix II flying fox species in 1988 and 1989, which negated the utility of the treaty as a wildlife management tool and necessitated more stringent trade control measures, through the transfer of seven *Pteropus* species to Appendix I and the listing of all other *Pteropus* and *Acerodon* species on Appendix II, in 1989.

The effectiveness of the recent CITES listing in reducing exploitation of flying foxes for international markets and reversing population declines depends on the commitment of resources in the United States and exporting countries to enforce the CITES trade prohibition and exercise CITES controls and carefully monitor shifts or increases in exploitation within the United States. Properly carried out, these activities promise to yield concrete results in conserving these species. Commitment of personnel and financial resources should be top priority by all countries harboring populations of these species.

Reference

Brautigam, A., and T. Elmqvist. 1990. Conserving Pacific Island flying foxes. Oryx 24(2):81–89.

United States Conservation Laws That Apply to Pacific Island Flying Foxes

by

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Introduction

Federal statutes and regulations dating back to 1900, placed restrictions on the taking, possession, or importation of various species of flying foxes. The Lacey Act,[1] passed by Congress in 1900, was one of the first Federal laws relating to wildlife protection. Among its provisions was a section to prohibit the importation of injurious wildlife, including an absolute ban on the importation of some live flying foxes. The intent of the law, which remains in effect to this day with limited amendments, was to prevent the establishment of foreign species by prohibiting the importation of stock that might colonize. This section of the Lacey Act was not intended to promote conservation of flying foxes. Subsequent amendments to other sections of the Lacey Act, most recently the Lacey Act Amendments of 1981,[2] were intended to promote wildlife conservation by prohibiting illegal interstate and foreign commerce in all wildlife, which, by definition, includes all flying foxes.

The Endangered Species Act of 1973[3] currently lists one species of Pacific flying fox (the Little Marianas, *Pteropus tokudae*) and one subspecies (the Marianas, *Pteropus mariannus*) as endangered. The little Marianas flying fox is believed to be extinct. The same act provides limited protection for several additional species or populations of flying foxes through their inclusion on Appendix I or Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora[4] (CITES). Effective 18 January 1990, seven species of flying foxes were listed on Appendix I of CITES[5]: Truk, *Pteropus insularis*; Marianas, *P. mariannus*; Pohnpei, *P. molossinus*; Mortlocks, *P. phaeocephalus*; Palau, *P. pilosus*; Samoa, *P. samoensis*; and Pacific, *P. tonganus*. All members of the genera *Acerodon* and *Pteropus* not listed on Appendix I were listed on Appendix II of CITES on the same date.

In addition, regulations contained in Part 14 of Title 50, Code of Federal Regulations, provide uniform rules and procedures for the importation, exportation, and transportation of wildlife.

Injurious Wildlife

The prohibition against the importation of flying foxes under the injurious wildlife section of the Lacey Act is found in Section 42 of Title 18, United States Code Annotated, and in Part 16 of Title 50, Code of Federal Regulations. The prohibition applies only to live members of the genus *Pteropus*. Any importation into or transportation between the United States and any territory or possession of the United States is prohibited, except for certain purposes and under certain conditions. Per-

1 18 U.S.C. §42(a)(1976), as amended by Lacey Act Amendments of 1981, Publ. L. 97-79, §9(d).

2 16 U.S.C. §3371-3378, Pub. L. 97-79, 16 November 1981, 95 Stat. 1073. For legislative history and purpose of Pub. L. 97-79, see 1981 U.S. Code Cong. and Adm. News, p. 1748.

3 16 U.S.C. §1531-1543, Pub. L. 93-205, 28 December 1973. For legislative history and purpose of Pub. L. 93-205, see 1973 U.S. Code Cong. and Adm. News, p. 2989.

4 TIAS 8249, 3 March 1973, Washington, D.C.

5 *Federal Register*, Vol. 54, No. 240, pages 51432-51437, Friday, 15 December 1989.

mits may be obtained from the Director of the U.S. Fish and Wildlife Service (Service) to allow the importation and transportation of live specimens for zoological, educational, medical, or scientific purposes.

Lacey Act Amendments of 1981

The Lacey Act Amendments of 1981, signed into law by President Reagan on 16 November 1981, established a single comprehensive statute to provide more effective enforcement of state, federal, Native American tribal, and foreign conservation laws protecting fish, wildlife, and rare plants. With the exception of a package-marking provision, none of the offenses under the Lacey Act stand on their own. In order to prove a violation of the Lacey Act, it remains necessary to first prove that there has been a violation of an underlying law relating to fish, wildlife, or rare plants.

The law, among its many provisions, makes it unlawful for any person subject to the jurisdiction of the United States to (1) import, export, transport, sell, receive, acquire, or purchase any wildlife taken or possessed in violation of any law, treaty, or regulation of the United States; or (2) import, export, transport, sell, receive, or purchase in interstate or foreign commerce any wildlife taken, possessed, transported, or sold in violation of any law or regulation of any state or in violation of any foreign law.

Two points must be understood. First, the underlying law or regulation must be related to wildlife conservation. For example, a Lacey Act prosecution cannot be predicated on a customs duty infraction. Second, the term "state" as defined in the act, includes Guam, Northern Mariana Islands, American Samoa, and any other territory, commonwealth, or possession of the United States.

Therefore, flying foxes, or their parts, that are imported into or exported from the United States or which are transported between any territory or possession of the United States must be in compliance with all applicable federal, state, or foreign wildlife conservation laws.

Endangered Species Act of 1973

Protective prohibitions that apply to those species of flying foxes which are listed as endangered under the Endangered Species Act of 1973 can be found in Section 1538 of Title 16, United States Code Annotated and in Part 17 of Title 50, Code of Federal Regulations. The prohibitions are broad. Without a permit it is unlawful for any person subject to the jurisdiction of the United States to import, export, transport, or ship in interstate or foreign commerce in the course of a commercial activity, sell or offer for sale in interstate or foreign commerce, or to take any endangered or threatened species. The term "take" is defined in the act to include such activities as harm, harass, pursue, hunt, shoot, wound, trap, kill, capture, or collect. The prohibitions apply equally to live or dead animals. Endangered species permits are issued only for scientific research and enhancement of propagation or survival of the species.

Commercial activities involving legally acquired endangered or threatened species that take place entirely within one state are not prohibited. Further, no permit is required to possess legally acquired endangered species. The term "state" is defined in the Endangered Species Act to include American Samoa, Guam, and the Trust Territory of the Pacific Islands.

CITES Convention

Another important aspect of the Endangered Species Act, particularly as it relates to the trade in flying foxes, makes it unlawful for any person subject to the jurisdiction of the United States to engage in any trade contrary to the provisions of the CITES Convention.

Regulations implementing CITES are found in Part 23 of Title 50, Code of Federal Regulations. Under these regulations, the United States established procedures to regulate the import and export of imperiled species covered by the Convention.

All shipments of Appendix I species (including parts and products) require two permits, one from the importing country (obtained first) and another from the exporting country. Import for primarily commercial purposes is prohibited. Permits are granted only when the import or export will not be detrimental to the survival of the species. In effect, the importation for food purposes of those species of flying fox now listed in Appendix I is prohibited.

Appendix II species may be imported without an import permit; however, a CITES export permit or re-export certificate from the exporting country must accompany each shipment. Appendix II export permits may be issued for any purpose as long

as the export or re-export will not be detrimental to the survival of the species.

CITES imposes no restrictions or controls on shipments between states or U.S. territories, including Guam, the Pacific Trust Territories, and American Samoa.

The United States recognizes an exception from CITES permit requirements for personal or household effects, not including live wildlife. Parts and products of Appendix II and Appendix III wildlife that are accompanying personal baggage or household effects may be imported into or exported from the United States without CITES documentation provided the reciprocal foreign country does not require a CITES permit or other certification for this type of export or import.

Importation and Exportation Regulations

In addition to the statutes and regulations previously discussed, Part 14 of Title 50, Code of Federal Regulations, contains uniform rules and procedures for the importation, exportation, and transportation of wildlife. Basic provisions include the establishment of a wildlife declaration requirement, restrictions on customs ports of entry through which wildlife may be imported or exported, and a licensing requirement for commercial importers who do more than $25,000 of wildlife trade annually.

There are broad exceptions, however, to the declaration requirement and to the designated port of entry requirement.

Except for wildlife requiring an import or export permit pursuant to Parts 16, 17, 18, 21, or 23 of Title 50, Code of Federal Regulations, wildlife products or manufactured articles that are not intended for sale and are worn as clothing or contained in accompanying personal baggage are exempt from the declaration and designated port requirements. A similar exception applies to wildlife being imported or exported through the port of Agana, Guam, if the wildlife has a final destination of Guam or if the wildlife originates in Guam. Wildlife not qualifying for one of the exceptions can be imported at a nondesignated port only under terms of a valid permit issued by the Service. Flying foxes listed in Appendix I of CITES, for example, cannot legally be imported or exported at Agana, Guam, without a nondesignated port exception permit. Flying foxes listed in Appendix II may only be imported at Agana, Guam, without a nondesignated port exception permit if the shipment qualifies for the CITES permit exception (e.g., accompanying personal baggage) and the flying foxes are not intended for sale. Importers and exporters who are granted a nondesignation port exception permit are required to pay an inspection fee for each shipment inspected by the Service. The fees normally are from $50 to $100 for each shipment.

Licensed wildlife importers and exporters must also pay a $25 user fee for each wildlife shipment regardless of the port of entry.

Summary

Flying foxes are afforded protection under two federal statutes, the Lacey Act Amendments of 1981 and the Endangered Species Act of 1973 and provisions of implementing federal regulations found in Parts 14, 17, and 23 of Title 50 Code of Federal Regulations. The Endangered Species Act of 1973 requires any person subject to the jurisdiction of the United States to comply with the provisions of the CITES Convention when engaging in the trade of flying foxes listed in CITES Appendixes.

Making the Conservation Laws Work

by

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Making the laws work, from my perspective, means preventing the wasteful killing of fruit bats. Although port inspection and confiscation of fruit bat shipments is one means for controlling and eliminating this trade, it is not the preferred way. Confiscated shipments are invariably composed of frozen bats. This illegal taking of fruit bats from Pacific islands is a no win situation for everyone. Some native plants lose an important pollinator, the importer and exporter both lose money in such transactions, and those interested in conservation of fruit bats also lose. In my opinion, enforcement of local bat conservation laws and regulations is the favored means for conserving this resource because it eliminates the killing of fruit bats.

It would not be difficult to make conservation laws work because Pacific Islanders are law-abiding and willing to enforce laws that protect their natural resources. However, such laws are unlikely to be enforced unless the Pacific island governments are involved in the decision-making process through which new laws are developed or old laws changed, and are kept fully informed regarding the need for any changes.

Each state or country should be held responsible for ensuring local compliance with the laws of other Pacific island states or countries. They should enforce those laws just as they would want their laws to be enforced. Any special data collection or other requirements should also be agreed to by the cooperating governments.

Some constituencies expressed concern regarding recent changes in fruit bat conservation laws and the appropriate enforcement. The lack of response to the laws could indicate this process has some serious problems. United States government sources, responsible for keeping local resource management agencies involved and informed, have not adequately fulfilled this critical duty. The recent change in listing of *Pteropus* from Appendix II to Appendix I of the Convention on International Trade in Endangered Species of Fauna and Flora (CITES) is a good example. None of the local governments that will be affected by this change (i.e., those that are expected to comply with the change) was informed of the proposed change or had any opportunity to provide input during the deliberations leading to the change. Pacific fruit bats would be better served with stringent enforcement of local prohibitions against taking rather than by a prohibition of entry into the United States (i.e., CITES restrictions), where they are intercepted as frozen carcasses.

A large part of this problem can be attributed to faulty communication. Most do not know the precise person or agency that needs to be contacted regarding a specific CITES-related issue. There is virtually no documentation available regarding the designated contacts for the various Pacific island governments. In Pohnpei State, Federated States of Micronesia (FSM), for example, who is the management authority, the scientific authority, the official contact regarding endangered species matters? This basic information is needed for all the Pacific island governments, not only for those involved in trade of fruit bats to the United States. This information base must also be maintained to ensure that it reflects any changes or modifications made at the local level, and is provided to those agencies or persons involved or concerned with resource management issues in this region.

If this function is to be performed by a U.S. agency, a greater effort must be made to keep all constituencies informed. If the agency is unable to

do this, because of lack of funds or staff resources, some alternative means for ensuring an uninterrupted flow of communications among affected and interested parties must be developed. A regional clearinghouse, for example, could be created to perform this function. This entity would keep current a mailing list of contacts, compile country information regarding regulatory requirements, disseminate this material to all regional representatives, and perform any other necessary tasks. Possible candidates for this post include Bat Conservation International, Inc. (BCI); The Nature Conservancy (TNC); U.S. Fish and Wildlife Service (Service), Region 1, Pacific Islands Office; or some combination of these.

All of the people at this conference are concerned with making conservation laws for fruit bats work. In order to accomplish this objective we need to establish some ground rules. First and foremost, we need to set aside personal biases and agendas and focus on the objective—conserving fruit bats throughout the Pacific region. In this context the commonly accepted definition of conservation is wise use. Wise use is achieved through the establishment and implementation of scientific resource management principles and practices. In addition to putting management of fruit bats on a sound basis, adequate consideration must also be given to the needs and desires of Pacific island states and their citizens. Although I personally have a strong bias against commercial exploitation of fruit bats, I firmly believe that any government interested in this trade should be given the opportunity to state its case before the idea is dismissed. Traditional subsistence use should be permitted, provided the fruit bat resources of a given state or country can sustain this taking. Subsistence take and commercial trade both must be supported by sufficient scientific data to ensure that the permitting of either activity will not be detrimental to the fruit bat resources of a state or country.

What kind of information will be required for making these important management decisions? First, we need to determine the population status of this resource in the various Pacific island states and countries. Furthermore, we will have to draw on the expertise represented by participants at this conference to determine the best census method for each specific political jurisdiction, and possibly, even specific areas as well. If no suitable census method is available, alternatives will have to be developed or an appropriate index adopted.

Second, many of the states and countries lack the funds and staff resources needed to obtain status information about fruit bat populations within their jurisdictions. Private organizations, such as Bat Conservation International, and government organizations, such as the Guam Division of Aquatic and Wildlife Resources and the Service, need to pool their resources to assist in filling this void. Technically trained staff could be provided by these cooperating organizations and agencies, while the requesting local agency could provide in-kind services such as interpreters and guides, government housing, joint use of vehicles, and so forth. This technical assistance should incorporate provisions for training of local resource agency staffs to enhance their internal capability for conducting these resource surveys.

Third, an advisory group, perhaps composed of representatives to this conference, needs to be created. The group would be available to provide technical assistance and advice regarding unresolved fruit bat issues. The group could consider and establish guidelines for such issues as defining traditional subsistence use, determining what constitutes significant crop depredations that would warrant control of local populations, and determining disposition of fruit bats taken pursuant to crop depredations or those that may be confiscated in violation of any law.

We can make fruit bat conservation laws work by respecting and supporting each other's laws, by consulting with states and countries that might be affected by amendments of old laws or creation of new laws, by ensuring that all affected and interested states and organizations are informed regarding any changes in conservation laws, by making conservation and management decisions based on the best biological information obtainable, and by communicating with others regarding fruit bat issues to resolve our differences. After all, it is in everyone's best interest to put Pacific-wide conservation of fruit bats on a sound basis.

Part 5.

Education and the Future

Suggestions for Long- and Short-term Education Strategies to Address the Conservation of Pacific Island Flying Foxes

by

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Introduction

The alarming population declines of Pacific island flying fox species in recent years, because of international trade for human consumption, initiated international pressure to provide increased protection and new management strategies. In 1989, seven species were added or upgraded to Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix I status, and 54 other flying fox species were placed in Appendix II (Brautigam and Elmqvist 1989). To assist with the implementation of new CITES regulations, the United States Fish and Wildlife Service sent two inspectors to Guam, the marketing center for Pacific flying foxes, to help regulate the importation of protected species (Graham and Murphy 1990).

Legal protection for threatened or endangered species is an important step to addressing endangerment and long-term survival. Public education is vital to sustained protection and management of these bats over time. Few groups of animals are so poorly understood and unappreciated as bats. Yet as plant pollinators and seed dispersers, they are essential to the maintenance of Pacific island forests.

Conservation education needs to play a major role in any protection or management plan. Only with increased knowledge about bats and appreciation for their importance to island forests, on which people depend, will there be a secure future for bats or their unique habitats.

This paper presents ideas for long- and short-term education strategies to raise awareness about bats. I will use examples to illustrate successful wildlife education programs in the Pacific, Latin America, and the Caribbean.

Long-term Strategy

A long-term strategy to develop awareness about bats should disseminate information to all segments of a target population or region, especially the next generation of children. It is an exciting and creative process with unlimited potential. Over a period of several years, the strategy seeks to establish bats as an integral part of any Pacific island environmental education program. Vital components of a long-term strategy include a planning team, planning goal, planning model, attitude survey, and information networking scheme.

Planning Team

Basic to any education strategy is a planning team and a well-designed, implemented and tested plan. To define and prioritize the problems for a wildlife conservation issue, people from the following categories should be invited to participate on a planning team.

1. *Biologists and Wildlife Managers*—These members are able to obtain information on the biology and ecology of bats and plants along with details of their current population status.
2. *Influential Community Leaders*—Community leaders can provide local influence as well as important socio-cultural perspectives vital to the success of any education plan.

3. *Motivated Educators*—Excited educators can breath enthusiasm, energy, and creativity into a project and can usually achieve great success with limited resources. These people will also be most involved with the sharing of information.
4. *Sympathetic Hunters*—Hunting wildlife may be culturally based, however, many hunters are interested in the sustainability of a wildlife resource and can provide valuable perspectives for hunter conservation ethics.
5. *Local Government-Tribal Officials*—Such individuals can help review and enforce existing legislation and assist with distribution of information.
6. *Local Environmental Groups*—Usually members of such groups volunteer their time and energy to help raise money and distribute information.

Planning Goal

The collective goal of a planning team organizing a long-term education strategy might be stated: to practically demonstrate how human actions—both individual and collective—affect the natural systems that sustain life, and to generate appreciation for the interdependence of the natural and human world.

Planning Model

The model for designing and implementing any education plan can be a simple three-step process.

Step 1. Define and prioritize problems.

Step 2. Design and implement actions.

Step 3. Evaluate and refine.

The most important step is number three, evaluate and refine. By evaluating the strengths and weaknesses of actions taken, a plan can be improved and made more effective.

Attitude Survey

In planning a long-term strategy it is of great value to include a survey, conducted within a variety of age and employment groups, to determine the attitudes and beliefs about bats in the target area. Before developing a list of recommendations for flying fox conservation actions in Guam, L. Sheeline (School of Forestry and Environmental Studies, Yale University, personal communication) conducted a knowledge and attitude survey of the Chamorro tribe toward flying foxes. Patterns of consumption and levels of conservation awareness or interest were examined. Information gathered helped to identify misconceptions that can be addressed in education materials, making them more relevant to what people believe. Morton (1990) conducted an attitude survey about bats in Costa Rica and was able to incorporate widely held misconceptions into a series of education materials that were developed. Repeat surveys 1–2 years later are helpful in measuring change resulting from education initiatives.

A Sampling of Long-term Strategy Actions

The following kinds of actions seek to build conservation ethics over time. Networking, inviting as many people as possible to assist in the distribution of informative materials, is vital. Anyone of any age or social standing can help.

1. *Prepare education materials.* It's important to develop a resource base of slide programs, posters, books, and pamphlets. These can be used by educators and the news media. For example, Bat Conservation International (BCI) of Austin, Texas, develops teaching materials and markets them at a modest price to cover costs. These materials are frequently purchased by bat enthusiasts and donated to favorite learning centers. BCI also produces inexpensive pamphlets for distribution and media kits for reporters and journalists.
2. *Conduct teacher training workshops.* Training teachers can greatly facilitate the mission of raising awareness in young people. A 1-day workshop is often enough to provide background information about bats and training in the use of educational materials. Educators who take a special interest in bats may want to form student clubs. BCI initiated a program of after-school bat clubs in Austin, Texas. In addition to learning about their biology, students were required to identify a problem for local bats and take collective action to try and solve it.
3. *Organize hunter education programs.* Educational programs offer opportunities to promote sustainable management of a threatened resource. When appropriate, programs can be a requirement for obtaining a hunting permit.
4. *Generate media attention.* Invite radio and television stations, reporters, and other journalists to cover local events and issues related to a bat

conservation problem. Regularly submit informative articles to the education section of newspapers or magazines. Butler (1989) sucessfully used the media to promote national pride in saving an endangered parrot from extinction. When public support grew, many local politicans aligned themselves with the issue and became spokespersons for the parrot's conservation.

5. *Train young people to assist with education and data collection.* Young people can easily learn how to educate others about bats. A 14-year-old boy in Texas has become a resident expert on bats and travels around the state and country giving presentations to large audiences. He and his bats were recently invited to appear on one of the most popular talk shows in the United States (Murphy 1989). Young people can also be helpful in gathering research data. In Colombia, A. Savage (Department of Psychology, University of Wisconsin, personal communication), a primate biologist, trained teenagers in a rural area to become field assistants for a tamarin project. They learned how to record population data and received classroom credit for their efforts. They also assisted with community education programs.
6. *Display exhibits.* Airports, banks, museums, nature centers, and libraries are excellent sites for attractive, photographic exhibits to raise awareness about a conservation problem. Since international trade is one of the main issues surrounding these endangered species, airports are excellent places to raise awareness.
7. *Create a natural history tourism industry. Intact forests and wildlife have great potential for ecotourism and tourist dollars.* Such an industry may take several years to establish but could offer long-term rewards. On the island of Dominica, a recent grassroots education campaign for the Sisserou (parrot) has resulted in an increased number of tourists wanting to see the beautiful bird, endangered because of the international pet trade (Begley 1989).

A primary barrier to education is almost always funding. Fortunately, grant proposals for education are now accepted by many international conservation organizations and foundations. Funds can also be solicited locally from the private sector. Butler (1989) was able to obtain corporate support on Dominica for parrot bumper stickers, and the local brewery named a beer after the Sisserou, and donates a portion of the proceeds to island conservation activities.

Short-term Strategy

Crisis Management

The conservation situation is urgent for many bat species. Critically small populations are extremely susceptible to natural catastrophe. In the Samoan islands, recent Hurricane Ofa stripped the island forests of foliage and fruit and posed a threat to two endangered bats. Their food resources destroyed, starving bats in American Samoa moved into urban gardens to feed. There, they were attacked by teenagers with slingshots—frequently just for fun. N. Daschbach (Le Vaomatua, American Samoa, personal communication) reported that thousands of bats were killed, despite a closed hunting season. Circumstances like these, require a short-term strategy or crisis-management approach, usually less than 2 years in duration.

When reacting to a crisis the public should be immediately notified about the situation. The quickest way to do this is through the media. The most popular and widespread communication media—newspapers, radio, or television—should be utilized first. Emphasis must be placed on targeting the population segment (such as teenagers with sling-shots) that may be causing the problem.

In American Samoa, the environmental group Le Vaomatua obtained a small grant from BCI and used the funding to heavily publicize the deliberate killing of thousands of fruit bats. For several weeks, they ran four radio spots a day in English and Samoan. Full page advertisements in both languages were published in the local newspaper along with articles about the episode (Figure). The government produced a free television spot (in Samoan) which featured a Samoan Batman asking people not to kill his relatives. Most of the media coverage was seen on the neighboring island of Western Samoa, also devastated by the hurricane. Many people then understood why bats were starving and set out food for them. A government agency translated a BCI slide program into Samoan and presented it to island mayors. Mayors were asked to help stop the killing, and it wasn't long before several of them personally turned in large numbers of slingshots to the agency office.

Forests eventually began producing again and bats left the urban areas. The government, Depart-

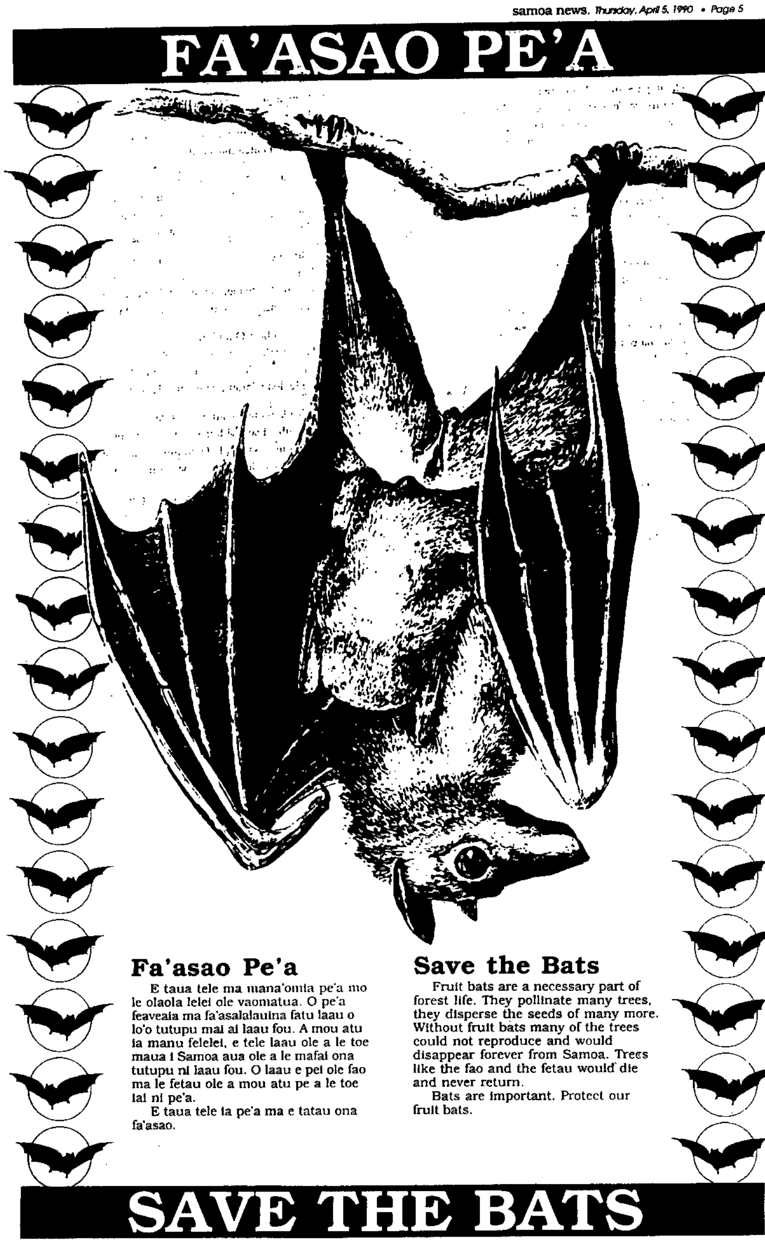

Figure. Newspaper advertisements were used to advertise the plight of bats ravaged by a hurricane that struck American Samoa.

ment of Marine and Wildlife Resources, cancelled the hunting season that year to enable bat populations to recover. Le Vaomatua and several government agencies will continue planning a long-term strategy to raise public awareness about bats. With a new understanding of bats, perhaps this kind of tragedy will never happen again in American Samoa.

The experience in the Samoan islands is an excellent example of a short-term, crisis-management strategy that was highly successful. The results of this campaign will be shared with other island areas in the Pacific and will enable them to be better prepared to address a similar situation. Spreading this type of information is vital to bat conservation education in the Pacific, especially when endangered or threatened species are involved.

Additional Ideas for a Short-term Strategy

Produce music video advertisements. The Butler campaign in the Caribbean produced videos using reggae, blues, and gospel music. The island's residents were dancing and singing about the endangered birds. An entertain-

ing approach to raising environmental awareness has wide appeal.

Advertise on billboards. Attractive billboards on busy streets are a great way to reach the public with a conservation message. A corporation might be enticed to pay the bill in exchange for a mention of what they are doing for the environment.

Utilize movie theaters. A theater owner might be willing to include a recorded conservation message and a few photographic slides during the previews of coming attractions before the main feature.

Request utility bill inserts. Le Vaomatua in American Samoa is making plans to include a small flyer about bats in phone bill envelopes. Other utility companies might be convinced to do the same. During a crisis, this would be an inexpensive and effective way to reach many households.

Conclusion

As world population increases, environmental problems become more severe. Technology hastens the process. Before the arrival of automatic weapons, freezers, and inter-island air service between Pacific islands, flying fox bats were not hunted to extinction. Worldwide, plant and animal species are becoming extinct at an unprecedented rate. The World Resources Institute states that 1.5 acres of tropical forest disappear each second. Solutions to these problems are highly complex. However, without adequate information, no problem can be addressed.

International organizations can be forerunners in collecting and providing such information. Time is growing critically short for too many species. We must not continually re-invent the wheel each time a new education strategy is designed. BCI is the world's resource center for information about bats and will collect and help distribute reports on education activities throughout the Pacific Region. In addition, BCI offers assistance in organizing and producing education materials.

Conservation education must become part of any protection or management plan. Only with people understanding relationships between the natural and human worlds is there hope for the future.

> Throughout the world, both educators and biologists strive to promote the conservation of native wildlife and environments by influencing people's actions and attitudes. While knowing relatively little about one another's programs, they attempt to solve some of the same issues in reaching the public with a strong and coherent conservation message. Through interaction with their colleagues, they will help to develop more effective strategies for fostering conservation actions among the audiences they serve. (Wildlife Conservation International's First Pan American Congress on the Conservation of Wildlife Through Education, Caracas, Venezuela, 1990.)

Conservation for Pacific island flying foxes is very hopeful, thanks to new legislation and the recent informative conference of which these proceedings were a part. New interest and enthusiasm has been generated to secure a future for these vitally important animals. Conservation education will play a key role in the long-term success.

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Flying Fox Action Plan

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The International Union for the Conservation of Nature and Natural Resources (IUCN)—The World Conservation Union—is a consortium of governments, government agencies, and nongovernmental organizations working cooperatively to conserve natural resources in the context of sustainable development. The Union's Species Survival Commission consists of more than 70 groups specializing in plants and animals from orchids to elephants. Other groups, such as the Trade Specialist Group, work across taxa in important areas of conservation concern.

The determination of conservation priorities has a long tradition within the Species Survival Commission, and currently these priorities are achieved by means of comprehensive action plans. These plans are the results of studies carried out by members of specialist groups. The plans include a thorough overview of all the species within their brief, a system of setting conservation priorities, and a compilation of proposed projects to address these priorities. The Chiroptera Specialist Group (CSG) consists of about 70 members worldwide, and its current priority is the preparation of a Flying Fox Action Plan. Those members who have first-hand knowledge of the general biology and ecology of particular species of the family Pteropodidae have been invited to provide species accounts that will document distribution, main food plants, breeding biology, threats, and occurrence in protected areas. The plan will also recommend conservation action. Invitations to contribute to the plan were first issued in mid-1989, and biologists are continually recruited to assist in this activity. As material arrives from contributors, it is collated by the plan coordinator, S. Mickleburgh, of the Fauna and Flora Preservation Society, myself, and CSG's secretary, T. Hudson. S. Mickleburgh's involvement is made possible by funding from the Zoological Society of London, the Jersey Wildlife Preservation Trust, the World Wildlife Fund, and the Species Survival Commission. Once the plan is assembled, IUCN will provide all printing and distribution costs.

Action plans are vehicles by which specialist groups' expertise can be harnessed and directed more effectively to identify priorities and implement conservation projects.

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